THE DEER OF THE WEYBOURN CRAG AND FOREST BED OF NORFOLK

BY

AUGUSTO AZZAROLI

(University of Florence)

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SYNOPSIS

The systematics of the Cervidae and the stratigraphy of the fossiliferous Pleistocene deposits of the Norfolk coast are clarified by a revision of material mainly in the A. C. Savin collection, in the British Museum (Natural History), and the John Gunn collection, in the Castle Museum, Norwich. Three successive faunas are distinguished in the Forest Bed Series. The nomenclature and relationships of various other fossil deer are also considered.

CONTENTS

INTRODUCTION

A REVISION of the Forest Bed deer has been needed for a long time. The descriptions of the most interesting specimens are scattered in the older literature : Falconer (1868), Dawkins (1887), Newton (1882), Gunn (1891), Harmer (1899). A few specimens were described more recently by Reynolds (1929–34), but these works refer mainly to the antlers, and no comprehensive study has been published. Moreover the series in the British Museum (Natural History) has been considerably enriched through the careful and long-continued work of A. C. Savin (1861–1948) of Cromer ; his first collection was acquired by the Geological Department in 1897, and his second in 1945.

The material examined consists of several hundred specimens, mostly in the Savin collection. I have further studied the important collection made by John Gunn (1801—1890), now in the Castle Museum at Norwich. There are in addition a few fossils of various origins in the two museums mentioned, in the Museum of the Geological Survey, in the Natural History Museum at Ipswich and in the private collection of Mr. J. E. Sainty of West Runton. I have not seen the material of other private collections, described by Dawkins (1887).

The fossils are highly mineralized, hard, and generally have a peculiar dark brown colour and a shiny surface; some of them, belonging to the older faunal elements (see later), are more ferruginous. Some are much worn, but for the most part they have a well-preserved surface. However, they consist almost exclusively of isolated bones. Only the skull of *Megaceros verticornis*, described as *Cervus belgrandi* by Harmer (1899), was found in connection with the first two vertebrae. This specimen is also exceptional in that the upper portions of its antlers are present. In the other specimens only the more resistant lower parts have been preserved. Most of them consist of lower portions of antlers, frontals, horizontal rami of mandibles, isolated teeth, limb bones and vertebrae. Brain cases are not uncommon, but no facial portions of skulls have been preserved, and maxillae are rare. Humeri and scapulae are represented only by the lower portions, except a heavy humerus of *Libralces reynoldsi*.

In the text I have used the abbreviations B.M. (G.D.) for the British Museum (Natural History), Department of Geology; G.S. for the Museum of the Geological Survey of England. The registered numbers of the specimens, when quoted in the explanations of the figures have not been repeated in the text. British Museum numbers preceded by the name Savin refer to his second collection.

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GEOLOGY

The Weybourn Crag and Forest Bed Series of the Norfolk Coast

The Weybourn Crag and Forest Bed series, described in Reid's classical memoir (1890), is exposed at the foot of the cliffs along the Norfolk coast for some miles east and west of Cromer, and the Forest Bed is exposed also over a short distance around Pakefield, near Lowestoft.   The cliffs consist of incompetent rocks—marine and freshwater gravels, sands and clays overlain by glacial drift, the whole resting on a levelled surface of chalk, and erosion is extremely rapid.   The exposures continually change, and Reid's work is an invaluable record of many years of survey, at a time when the lesser development of coast defences made observation easier. Study of the stratigraphy is made difficult by rapid lateral changes, by breaks in the sequence, and by the discontinuity of outcrops.   In many places the contorted glacial drift has disturbed this series, or cut it down to the chalk.

The marine and freshwater series, to summarize Reid's data, rests on the chalk. At the junction the surface of the chalk is covered by a " stone band " of large unworn or little-worn flints; this stone band represents no stratigraphical horizon. In the country around Cromer it is overlain by the " Weybourn Crag," a false-bedded shelly sand alternating with laminated clay.   This crag generally occurs in patches on the stone band, beneath high tide-mark, between Weybourn and Trimingham.   It " has been traced continuously from Cromer to Weybourn, except for short distances, where it is cut out by channels of the estuarine Forest Bed, or has been ploughed out by glacial action, so that the Boulder Clay rests immediately upon the Chalk " (Reid, 1890: 139).   In a section at East Runton it yielded a rich fauna of molluscs and some mammal bones.   In isolated outcrops its distinction from the Forest Bed is sometimes difficult, so that many authors overlooked its occurrence.   Towards the south-east the Weybourn Crag becomes more clayey and probably passes laterally into the Chillesford Clay, which in this section of the coast has been found only in borings, at Mundesley and possibly at Happisburgh.

The Forest Bed series covers unconformably the Weybourn Crag and has always a more or less gravelly base.   Probably there is a land surface between these two formations, " for in one place the Crag has a rather weathered appearance; but of this one cannot be certain " (Reid, 1890: 149).

The Forest Bed series is in three divisions: a " Lower Freshwater Bed," composed of carbonaceous clays, silt and loam; an "Estuarine Bed" or Forest Bed *sensu*

stricto, composed of false-bedded carbonaceous sands and laminated clays with mammal bones and drifted tree-stumps; and an " Upper Freshwater Bed," composed of peaty clays and sands.   The discontinuous Lower Freshwater Bed is very seldom preserved, and its observation to-day is still more difficult than at the time when Reid saw it on the shore north west of Cromer, where it cut through the Weybourn Crag (1890: 159), and at Trimingham (1890: 163).   The Estuarine Bed is practically continuous.   The Upper Freshwater Bed is somewhat variable in facies and its identification is not always easy.   It also is discontinuous and is separated from the estuarine division by an eroded and deeply weathered surface.

The Occurrence of Mammals

Many of the mammalian remains were found loose on the beach, especially after storms.   Some, however, were actually extracted from the rock *in situ*.   As a rule they were said to come from the Forest Bed, *sensu lato*, which is still considered the chief mammal-bearing horizon; but in the course of the present work it has become apparent that they are of different ages, so that their occurrence needs more careful discrimination.   Most of the fossils I have examined were obtained by A. C. Savin of Cromer, who collected for more than fifty years and gave accurate indications in his catalogue.   The specimens I have determined are said to come from the Forest Bed at W. Runton, E. Runton, Cromer, Overstrand, Sidestrand, Trimingham, Mundesley, Bacton, and Pakefield; from the beach at Palling and from the Upper Freshwater Bed at West Runton.   A single specimen, a fragment of a lower jaw of *Megaceros dawkinsi*, is said to come from the Weybourn Beds at Weybourn.   The specimens from other collections were all stated to come from the Forest Bed, partly from the same localities as Savin's, partly from other localities, such as Ostend, Happisburgh, the Walcot gap, and Hopton.   However, not seldom there is only the indication " Forest Bed; Norfolk."   A few specimens were dredged off the coast and on the Dogger Bank.

It is remarkable that Savin did not distinguish an Upper Freshwater Bed in many localities where it has been recorded by Reid; possibly he was misled by differences in facies from the corresponding bed at West Runton, and as a matter of fact the distinction of these horizons in the field is not always easy.   Savin distinguished a Lower Freshwater Bed at East Runton, and Weybourn Beds at East Runton and West Runton, but recorded from them only fish remains.   Here too he was probably misled by the common belief that mammal remains occurred only in the Forest Bed and Upper Freshwater Bed.   But, as stated above, Reid found mammal bones also in the Weybourn Crag, at East Runton.   Finally, Savin's attribution to the Weybourn Crag of a lower jaw from Weybourn might be based merely on the locality and might be equally incorrect.

The mixed character of the " Forest Bed Fauna " led me to suppose that its members came from different horizons.   The characters of the fossils, consisting of large and well-preserved antlers of deer, rules out any possibility that they were washed in.

The distribution of the species I have studied shows that there is no sharp break

between the fauna of the estuarine Forest Bed and that of the Upper Freshwater Bed, which, according to my correlations, belong to the great Mindel-Riss interglacial (see later, section " Chronology "), whereas an older fauna may be sharply distinguished.   There is no doubt that it came from an older horizon, separated from the estuarine bed by a remarkable gap.   The widespread occurrence of this fauna, as well as the high ferruginous content of most of its specimens, rule out the Lower Freshwater Bed, whilst the Weybourn Crag corresponds to what may be expected to be their matrix.   In fact, most of Savin's specimens are said to come from the gravel pans and sands on the shore, at some distance from the cliffs ; and Mr. Sainty of W. Runton has in his private collection a beautiful lower jaw of *Libralces gallicus*, a typical representative of this earlier fauna, which he extracted from a patch of shelly crag directly overlying the stone band, on the shore between West Runton and East Runton, below high tide-mark.   This crag, still occurring in patches but variously exposed owing to the rapidity of erosion, corresponds to Reid's description of the Weybourn Crag.

Boyd Dawkins, who certainly was not influenced by prejudices about the stratigraphy, referred a skull of the same species from the Savin collection (1887, pl. 1, fig. 1) to the " Weybourn Beds (Forest Bed Series), East Runton, Cromer." Savin's catalogue gives for this specimen the sole indication " East Runton Forest Bed."

These older species were found only in the western section of the coast, between Sidestrand and West Runton, where the Weybourn beds are exposed.   Very few specimens came from Mundesley, where the Chillesford Clays are concealed beneath the beach.

THE PHYLOGENY OF THE CERVIDAE

The early history of the deer is little known.   Probably they achieved the greater part of their evolution in Asia and North America, where the record is fragmentary and very scanty, during the Pliocene.   In Europe their history is largely one of successive waves of immigration and replacement.   Their classification is therefore vague.   Simpson (1945) did not give an exact picture of the phyletic relationships : for instance, his *Odocoileinae* are not a phyletic unit, neither are his *Cervinae* except in so far as living species are concerned.

In practice only restricted groupings of related genera can be established ; the precise rank of these higher taxonomic units is largely a matter of taste.   They may be called without prejudice subfamilies.   Among the living deer seven subfamilies are recognized : *Cervinae, Muntiacinae, Odocoileinae, Capreolinae, Rangiferinae, Alcinae, Hydropotinae*.   As yet hardly any other taxonomic categories within or above these subfamilies can be established, and if we take into account also the fossil forms, things become more difficult.

The present work is concerned only with the *Cervinae, Capreolinae* and *Alcinae*.

The Capreolinae *and* Alcinae

The history of the *Capreolinae* is quite obscure.   Some Miocene forms have been tentatively referred to this group, but they are poorly known (Azzaroli, 1948 :

46 ff.), and, so far as I am aware, there is no record of this subfamily during the Pliocene. The dental characters vaguely suggest some affinity with the *Alcinae*.

The *Alcinae* are represented in the Quaternary by three genera, *Alces*, *Cervalces* and *Libralces*, closely similar in the characters of the dentition and limb bones, but widely divergent in the skull. They are practically unknown in the Pliocene, but were already differentiated in the Pontian, where they are represented by *Alces maeoticus*.

The Cervinae

The problem of the *Cervinae* is less simple, and requires more explanation. In 1948 I stated that they were derived from the Pontian *Pliocervinae* of S.E. Europe and China; the definition of the *Pliocervinae* was based on Zdansky (1925, 1927). A study of the works of Alexejew and Khomenko on the Pontian deer of S.E. Europe necessitates some modification of this statement.

(a) *The Pontian deer from S.E. Europe*

In 1913 Alexejew named *Procervus variabilis* from Pontian deposits near Petro-viêrovka, S. Russia. A more complete description followed in 1915. This species is distinctly smaller than a fallow deer; its teeth are brachyodont, the upper molars have a discontinuous cingulum, and the lower molars a well-developed *Palaeo-meryx*-fold. Varying with the individual, P_4 is either primitive or advanced; the upper premolars are primitive and the upper canines relatively strong. The skulls are badly damaged but seem to be of a primitive, rather unspecialized type. The brain cases are long, the supraoccipital crests weak. The pedicles are set obliquely and form two ridges at the sides of the forehead. The antlers, of various ages, are short, stout and much flattened; their form is irregular and extremely variable. They consist of a flattened, very strong brow tine, sometimes bifurcated at the top; and a short beam, gradually expanding upwards into a narrow palmation, ending in two to six small tines. The surface is deeply grooved. The first bifurcation takes place near the burr and eventually a small accessory tine is given off from it. The antlers of younger individuals are forked, and in the first stage they consist of simple prickets. The limb bones are primitive. The shaft of the ulna is strong, the upper epiphyses of the radius and tibia are small, and the fore limb has complete lateral metacarpals, with a well-developed articulation for the corresponding toes.

In 1914 Khomenko published a description of some Pontian deer from Taraklia, Bessarabia. His material was scanty and fragmentary, nevertheless he founded on them three new genera and species, *Cervavitus tarakliensis*, *Cervocerus novo-rossiae*, *Damacerus bessarabiae*, based on antler characters. Khomenko's specimens also included some teeth; they showed slight differences which he supposed to be specific characters. On these three genera Khomenko founded his new subfamily *Pliocervinae*.

Khomenko's genera have been variously accepted. Zdansky (1925) supposed that *Cervocerus novorossiae* and *Damacerus bessarabiae* were synonymous; Simion-escu & Dobrescu (1941) accepted the specific distinction only, and determined other

specimens from Bessarabia as *Cervocerus bessarabiae*. Simpson followed these authors and recognized the genera *Cervavitus* and *Cervocerus*, and included *Damacerus* in the latter.

However, there is little doubt that Khomenko's genera and species are all synonymous. The differences between the antlers are due to growth stages, and the teeth do not differ by more than individual characters. The choice for the generic and specific names is thus open, and here we shall adopt *Damacerus bessarabiae*. Its holotype is the antler figured by Khomenko (1914, pl. 4, fig. 6), the only one of Khomenko's specimens that is fully grown.

The deer from Petroviêrovka is closely related to this. The teeth are indistinguishable; P_4 displays the same fluctuations. The frontals, too, seem to be very similar, and the only marked differences lie in the antlers. In *Damacerus bessarabiae* they are less flattened, the brow tine is smaller and the first bifurcation is set high above the burr. It is consistent therefore to attribute these two species to the same genus. *Procervus* is preoccupied and the valid name is *Damacerus*, which will include therefore two species, *D. bessarabiae* (the genotype), and *D. variabilis*.

(b) *The Pontian deer from China*

In 1925 and 1927 Zdansky identified with Khomenko's *Cervocerus novorossiae* some deer of various Pontian localities in China. Other specimens from Shansi were referred to the same species by Teilhard & Trassaert (1937). These identifications are incorrect. The Chinese deer show only superficial similarities to those of S.E. Europe, but at the same time they display differences showing that they belong to completely different lineages.

The Chinese so-called *Cervocerus novorossiae*, as defined by Teilhard & Trassaert [Zdansky's description is sometimes vague and partly contradicted by his figures; moreover some of his attributions are questionable (see Teilhard & Trassaert, p. 38)], is a species of slightly larger size than the European *Damacerus*. Its skull is rather primitive; the pedicles form two prominent ridges on the sides of the forehead. The lacrimal pits are large and deep. The antlers are three-tined, cylindrical, and display a great variability in the position of the first bifurcation and in the length of the beam. Teilhard & Trassaert distinguished a " short type," with a straight beam, and a " long type," with a gently curved beam; they are linked by intermediate forms. The dentition is brachyodont. P_4 is primitive and there is no trace of the *Palaeomeryx*-fold on the lower molars. The upper premolars have the inner wall split, and a strong cingulum is stated to occur in the upper molars, but this is not to be seen in the figure. There are two complete but very thin lateral metacarpals, with rudimentary epiphyses.

With the possible exception of some more flattened antlers (pl. 5, figs. 1, 2), Zdansky's *Cervocerus novorossiae* corresponds on the whole with this species. According to him the cingulum is variable in the upper molars, and in the lower molars he described what he regarded as the remnants of a *Palaeomeryx*-fold: " Es handelt sich meistens um eine, vorn mehr oder weniger scharf begrenzte Rinne. An nur

ganz wenigen Zähnen ist eine solche nicht zu konstatieren." This is somewhat vague, but there is certainly no typical *Palaeomeryx*-fold, and no trace of it can be seen in the published photographs.

Zdansky also included in the *Pliocervinae* the genus *Procapreolus* Schlosser, the validity of which has been questioned by Teilhard & Trassaert. The latter authors, on the other hand, described a *Cervavitus demissus* whose generic identity with the European forms is no less questionable.

(c) *The relationships of the Pontian* Cervinae

In conclusion, in the Pontian, apart from some smaller forms more or less closely related to the *Muntiacinae*, and from the *Alcinae*, the *Cervidae* were already represented by two well-differentiated groups, namely the European *Damacerus*, with two species, and the Chinese three-tined deer, seemingly belonging to one species, for which new generic and specific names are required. They differed in the characters of the antlers, of the dentition, and of the fore limbs. These characters enable us to make some partly hypothetical inferences about their relationships.

In its dental characters the European *Damacerus* is closely related to the two-tined Miocene deer, and may have been derived from a genus with a well developed burr, e.g., *Euprox* (for full references on Miocene deer see Stehlin, 1939, with bibliography).

In my opinion the value of the *Palaeomeryx*-fold has been underestimated. It is supposed to have gradually disappeared by the end of the Miocene, but there is no evidence for this assumption. Throughout the Miocene it does not show any tendency to become reduced or to fluctuate, and it is still uncertain whether it has really vanished, or has been wiped out by the extinction of the species that bore it. A solution to this question might possibly be afforded by *Cervus ramosus* Croizet & Jobert (1826–28, fasc. 5, pl. 5, fig. 2). The age of the type is uncertain, but the same species occurs in the Villafranchian of St. Vallier-sur-Rhône and of Villaroya ; there is no trace of the *Palaeomeryx*-fold in its lower molars. A more primitive variety, *Cervus ramosus* var. *pyrenaicus*, which might perhaps be the ancestor of the typical form, was described by Depéret (1897 : 99–112, 124–125) from the Upper Pliocene of the Roussillon. Among the many lower jaws which can be attributed to this variety, there are specimens with a distinct *Palaeomeryx*-fold and specimens without any trace of it. I am unable to state whether there are intermediate conditions, nor whether all these jaws belong to the same species ; this however is highly probable, because the other deer from the Roussillon (Depéret's *Capreolus australis* and *Capreolus ruscinensis*, but actually belonging to one species) are much smaller. If so, *Cervus ramosus* would afford a good example of the *Palaeomeryx*-fold disappearing by fluctuation.

In the three-tined Pontian deer from China there was no *Palaeomeryx*-fold. P_4 was more primitive than in the European deer of the same age; the upper premolars were rather molarized, but this character always seems to be very variable and its significance is not quite clear.

This is all that is known of the Upper Miocene ancestors of the *Cervinae*. A

large part of them very probably originated from the Chinese species, and the lineage represented in the Pontian of S.E. Europe may possibly have survived with *Cervus ramosus* up to the Lower Pleistocene.

(d) *The Pliocene and Pleistocene* Cervinae

The history of the *Cervinae* during the Pliocene is obscure. Besides *Cervus ramosus* and its small relative from Roussillon, which might be related to *Damacerus*, several species of quite uncertain affinities are known. Most of them were found in the Montagne de Perrier and other localities of France. There is no evidence that any of them survived into the Pleistocene.

It would be consistent to give each lineage a distinct generic name, but the use of the name *Cervus*, although improper, cannot be dispensed with as long as these species are so poorly known. However, the name *Anoglochis*, originally proposed by Bravard, Croizet & Jobert, might perhaps be adopted for *Cervus ramosus*.

At the beginning of the Quaternary we find that the various genera which compose the subfamily are already differentiated, although in many cases represented by relatively primitive species. *Euctenoceros* and *Megaceros* make their first appearance in the Red Crag of East Anglia, *Euctenoceros* also in the Dutch Poederlian (see later), *Dama* in the Villafranchian of Tuscany (Azzaroli, 1948), *Rucervus* in the Pinjor stage of the Siwalik hills (to be described in a forthcoming paper by the author), *Rusa* in the Sanmenian of Nihowan (Teilhard & Piveteau, 1930), *Sika* in Chouk'outien and other Pleistocene localities (Young, 1932), *Axis* in the Lower Pleistocene of Shansi and Java (Teilhard & Trassaert, 1937; Stremme, 1911); *Cervus* s.str. makes its first appearance in the second interglacial of Europe. *Elaphurus* is doubtful in the Sanmenian of Nihowan, but has been identified in the Pleistocene of Japan (Matsumoto, 1915), and is represented also by a subfossil species at Anyang, N. Honan (Teilhard & Young, 1936). *Przewalskium* alone is not known as a fossil. There are in addition some primitive and poorly known species which cannot be fitted into any of these genera: " *Cervus* " *rhenanus* from Tegelen, " *Cervus* " *perolensis* from the Auvergne (Bout & Azzaroli, 1953), " *Cervus* " *punjabensis* and another species from the Upper Siwaliks (to be described in a forthcoming paper), and " *Cervus* " *philisi* from Sénèze (Schaub, 1942).

Many of these genera and species may have been derived from the Pontian three-tined deer of China; but some highly divergent genera, as, e.g., *Elaphurus* and *Megaceros*, are very probably of a quite different origin.

THE DEVELOPMENT OF THE ANTLERS

(a) *General Considerations*

Much has been written on the growth of the antlers, but our knowledge on this point is not entirely satisfactory. Each species and genus has its own peculiar pattern of antlers, obviously determined genetically, but the mechanism by which this pattern is brought into existence is practically unknown. Wislocki and others (1946, 1947) have studied the innervation and the process of ossification. It has

been established that the form of the antlers is not influenced by the course of nerve fibres, and attempts to explain the form of the antlers by the course of blood-vessels (see literature in Wezel, 1949) are equally unsatisfactory.   Moreover the antlers display an individual variability of form and size that cannot be explained by the action of genetic factors alone.   There is evidence that more factors, partly genetic, partly purely mechanical, influence the determination of their form. Huxley (1932) established that their size is controlled by a complicated allometric law, varying from species to species.   It is known, too, that increase in size of the antlers, within a species or subspecies, is followed by a more complicated ramification.   Inasmuch as this phenomenon occurs among individuals of the same genetic constitution, or even in successive growth stages of the same individual, it cannot be because of genetic differences, but rather because of purely mechanical factors: the antler tissue, growing from the top of the pedicle, seems to be unable to develop indefinitely in cross-section, but tends to divide as soon as it has reached a certain limit of bulk.   A closer study of this phenomenon is obviously outside the province of palaeontology.

In the recent deer, division generally takes place dichotomously, with the first bifurcation or bifurcations in a nearly longitudinal plane.   This led Pocock (1933) to formulate his theory of dichotomous growth; but it may be shown that this law is not general.

Each species obviously has its own range of variation, and eventually its particular type of asymmetry, as, e.g., the reindeer.   Broadly, the species with more complicated antlers are also the more variable.   Very much has been written on the variability of antlers, especially of the red deer; one of the most recent accounts has been given by Wezel (1949).   Allowance must however be made for the unnatural conditions under which red deer very often live (inbreeding, artificial selection, unfavourable or exceedingly favourable environment).   In deer living under natural conditions the range of variation is not so wide.

(b) *History*

If we trace back the history of the deer we may form a mental picture of the primitive conditions of the antlers, and of the way the more advanced features gradually became established.

No continuous phyletic line of an appreciable length has yet been ascertained. The principle of parallel evolution, recently exposed and discussed by Merla (1949: 117 ff.), will be extensively applied here.   This implies the more general principle of evolution controlled by internal factors, the validity of which has been questioned by many recent authors who hold a purely " Darwinian " point of view. The reasons for the interpretation accepted here have been discussed at length by Merla (1949) and by Watson (1949).

In my opinion the principle of evolution directed by internal factors is the only one to give a satisfactory explanation of the phyletic development of antlers.   It could be argued that their development might be controlled by factors linked with characters under selective control; this interpretation however gives no explanation

for the numerous instances of parallel evolution, nor for the polymorphism of antlers, which is in striking contrast with the uniformity of the other body characters.

Apart from the evolution of antlers, there are not many clear examples of ortho-evolution of characters which are surely not under selective control. A spectacular exception is the pachyostosis of the skull of *Megaceros*.

Lower and Middle Miocene: the primitive antlers

True *Cervidae*, shedding their antlers, made their first appearance in Europe during the Burdigalian and remained very primitive during the Helvetian and Tortonian (for full reference see Stehlin, 1939). They form a polymorphic group. Complete and well-preserved skulls are not known, but great differences are displayed in the position of the pedicles, and in many cases there is no typical burr. But one common feature is apparent: the antlers never grow in the form of prickets. Even in the earliest stages they tend to divide, taking the form of an irregular crown (*Stephanocemas*; in fact the form is somewhat intermediate between a crown and a fork), a fan (*Palaeoplatyceros*) or a longitudinal fork (*Heteroprox, Dicroceros, Euprox*). In Asia some of these forms survived into the Pliocene, and may perhaps have given origin to the living *Muntiacinae*.

Pontian. The emergence of modern types

A trend towards the formation of a beam became apparent in the Pontian. *Amphiprox*, from Eppelsheim, was still very primitive, with short antlers consisting of a straight beam and a very small brow tine, branching off high above the burr; but at the same time, deer with more complicated antlers lived in the S.E. of Europe and in China. They all had a distinct burr and a branched beam.

Damacerus is probably closely related to the earlier European deer. *Damacerus variabilis* seems to represent the most primitive condition. The differentiation between brow tine and beam is not very well established: they are both flattened, the brow tine is relatively large and bifurcated at the top. The general form of the antlers is very variable and irregular. The antlers of young individuals consist of prickets, but it is questionable whether the ontogenetic development actually reproduces the phyletic history. The formation of the pricket might be due to the action of genetic factors, normally leading to the formation of the beam, which in the youngster are not counterbalanced by a sufficiently strong tendency towards ramification, owing to the small size.

Damacerus bessarabiae is more advanced. There is a typical beam and a much smaller brow tine. The first bifurcation is set rather high above the burr, and in my opinion this should be considered an advanced character. The point, however, is not quite clear, and palaeontological evidence of the evolution of later forms (see, e.g., *Dama nestii nestii* from Olivola and the Upper Valdarno; Azzaroli, 1948) may seem to contradict this assumption. As a matter of fact, genetic and mechanical factors trending in opposite directions interact. The upwards shift of the first bifurcation is determined genetically, and the downwards shift during onto-genetic development is certainly due to a purely mechanical factor, the larger bulk

of growing tissue inducing earlier bifurcation. This factor also may eventually act in phyletic evolution. Moreover, a third character, namely, the opening of the angle of the bifurcations, seemingly under genetic control, may also interfere; this, however, seems to have become felt only after the end of the Miocene.

In the three-tined Pontian deer of China the antlers consisted of a cylindrical beam and cylindrical tines. They are rather variable, both in length and in the position of the first bifurcation. It has been stated in the preceding section that some palmated antlers figured by Zdansky might perhaps belong to another species.

Pliocene and Quaternary. New evolutionary trends

Although the antlers of these primitive deer were relatively small and simple, they were very variable. No attempt will be made here to explain this, but in later forms the patterns of antlers became more constant. New features appeared, as bifurcations at an obtuse angle, helicoidal tortion and undulation of the beam and tines, peculiar types of spatial arrangement of the branches (e.g., on a spherical surface in *Rucervus*, on a plane in *Euctenoceros*), or branching of the tines.

The flattening of the beam and tines is a very common feature. In some cases it may be a secondary appearance, but its phyletic origin is not always clear. This is true also of the palmation. In some instances, e.g., *Alces alces*, no sharp distinction can be traced between palmated and non-palmated antlers.

(c) On the Homologies of the Tines

The discussion of the formation of antlers leads to the question of the homologies of the tines. Some words on this problem are necessary because too rigid an interpretation of the homologies would be misleading.

After considering the work of other authors, Pocock (1933) proposed an interpretation of the homologies based on the theory of dichotomous growth. This can be summarized as follows. The primitive condition is assumed to be represented by the pricket. In the next stage it divides into an anterior and a posterior tine (a^1 and p^1). These two tines may have the same potentiality of growth and further division: this happens, e.g., in *Elaphurus* and *Blastocerus*. But generally p^1 is the stronger and divides into a^2 and p^2; then p^2 divides into a^3 and p^3, etc. In accordance with this principle Pocock established the homologies between the tines of all the living genera of the *Cervidae* and many fossil forms. In the particular instance of the red deer the bez tine normally occurs but is not constant; this was interpreted as having originated from the division of the brow tine.

In 1948 I fully accepted Pocock's views, but I now realize that rigid application of them is not possible. This theory however has the merit of having shown that there is no fundamental difference between beam and tines.

It has been shown above that the pricket is not the primitive condition, and that in the earliest stages branching is more or less irregular. As a matter of fact at the beginning the tines have no morphological individuality, that is, they cannot be compared to an organ such as a tooth. What is inherited is the general pattern of antlers. As this pattern gradually evolves, the beam and the tines acquire a

certain degree of individuality, which, however, is not absolutely fixed.   The evidence for this is that the eventual suppression of a tine, or the presence of accessory tines or even an accessory beam (a not uncommon occurrence in the red deer and reindeer), does not alter the fundamental pattern of the antler.   The example of the tamin (Fig. 1) is also instructive.   In this species, the surface of the antlers is sometimes very scabby; the tines (except of course the brow tine) are small, and no sharp distinction can be traced between the smaller tines and the larger asperities of the surface.
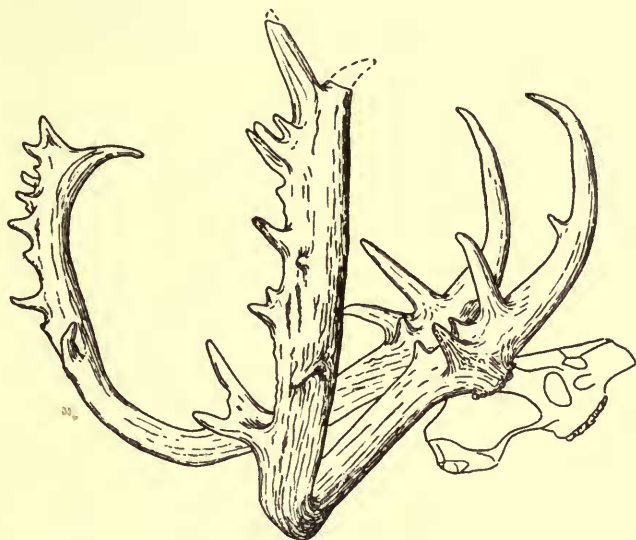

FIG. 1.   *Rucervus eldi*.   B.M. (Zool. Dept.), no locality.   ⅛ natural size.

True homologies can be established only between related forms, in which the evolution of the antlers has followed the same path.   It is meaningless to argue whether the homologue of the brow tine of, say, a fallow deer is represented by the small inner tine of *Odocoileus*, or by its bifurcated anterior tine, which in turn is obviously homologous with the anterior tine of *Blastocerus*; or to look for the homologue of the bez tine of the red deer in the reindeer and in the giant deer.

SYSTEMATIC DESCRIPTIONS

Genus *LIBRALCES* Azzaroli

In another paper (1952) I have established the new genus *Libralces*, with genotype *L. gallicus* from the Upper Villafranchian of Sénèze.   This species is present also in the Lower Quaternary of the Norfolk coast, together with three other species of the same genus.   These are more imperfectly represented, and are distinguished mainly by their size.   The distinction of the dentitions is easy, but greater difficulties arise in determining other remains, for the most part imperfect fragments

of skulls and antlers.   The attribution of some of them will therefore remain uncertain.   The limb bones that can be attributed to this genus are scanty.

I have defined the genus *Libralces* as follows (1952 : 134): skull broad, depressed and heavily built; forehead broad; antlers palmated, with a long beam directed horizontally outwards and gently curved.   Nasals long, articulated with the premaxillae.   Upper canines presumably present in the genotype, molars and premolars brachyodont, lower molars with strong basal columns; traces of the *Palaeomeryx*-fold in M_1, eventually also in M_2; P_4 as in *Alces*.   Forelimb telemetacarpal, size large.

Libralces gallicus Azzaroli

(Figs. 2, 3, 4 B, 5 A, 9 B, 10 D.)

1887. *Alces latifrons* (Johnson) Dawkins (pars), p. 1, pl. 1, figs. 1, 3 ?, 5.
1931. *Alces latifrons* (Johnson) : Roman & Dareste, p. 1256.
1944. *Alces latifrons* (Johnson) : Schaub, p. 285.
1952. *Libralces gallicus* Azzaroli, p. 134.

Summary Description of the Holotype and Paratype

The type of this species, a complete skeleton of a full-grown male, and a second incomplete skeleton were found in the Upper Villafranchian of Sénèze.   The original description may be summarized as follows: A species of large size, but distinctly smaller than the living elks.   The skull is broad and depressed, with a broad forehead and a very thick roof.   The face is proportionately less developed than in *Alces* and is characterized by the long nasals, which are articulated with the premaxillae.   The lower molars bear well-developed basal columns, and the first lower molar has a distinct groove on the hinder surface of its antero-external crescent. The antlers consist of a long, slender beam, directed horizontally outwards and gently twisted, which ends in a small palmation, set obliquely to the axis of the body, with small tines on its edge like *Alces alces*.   The limb bones are slender and differ from those of *Alces* only by their smaller size.   The neck is relatively long.

The Specimens from the Norfolk Coast

OCCURRENCE.   All the specimens that can be identified with certainty were found at East Runton and Sidestrand.   Imperfect specimens, whose identification is somewhat doubtful, were found at West Runton, Cromer and Pakefield; the last are much rolled.

DESCRIPTION.   The best specimen is represented by a brain case with its left antler, originally figured by Dawkins (1887, pl. 1, fig. 1).   In Azzaroli (1952, pl. 15, fig. 2) and in Fig. 2 the antler has been omitted.   An adult, or nearly adult antler from Sidestrand (Dawkins, 1887, pl. 1, fig. 5) and two antlers from East Runton can also be attributed to this species.   All these specimens show a rather narrow range of variation.   The more robust antlers (Fig. 5A, and Dawkins' fig. 1) tend to develop shorter beams.

A second brain case (Fig. 3), mentioned also by Dawkins, very probably belongs
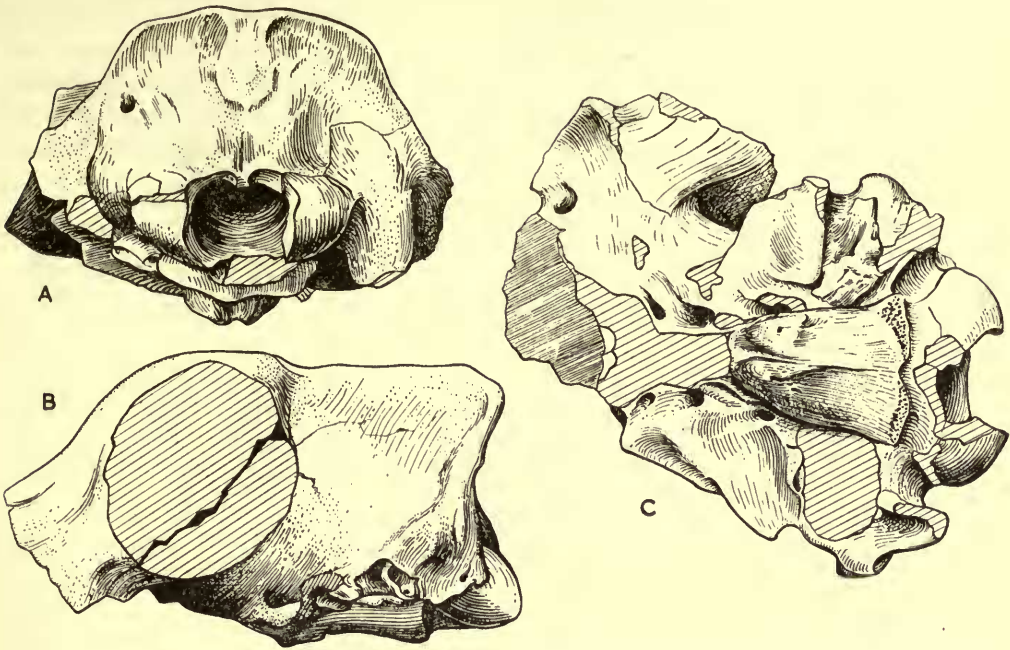
FIG. 2.   *Libralces gallicus*, skull from East Runton.   B.M. (G.D.), M. 6101.   ⅛ natural size.   (Specimen figured by Dawkins, 1887, pl. 1, fig. 1, and by Azzaroli, 1952, pl. 15, fig. 2.)   A, occipital view ; B, lateral view ; C, basal view.
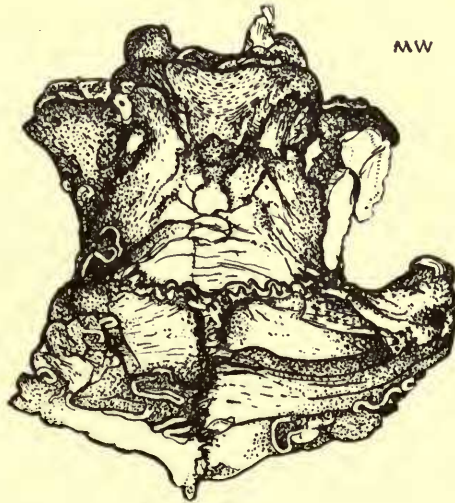

FIG. 3.   *Libralces gallicus?*   Skull of a young specimen, dredged off the Dogger Bank.   B.M. (G.D.), 46108.   ⅛ natural size.

to the same species.   It was dredged off the Norfolk coast and is highly mineralized, like the other fossils from the Weybourn Crag and Forest Bed.   This brain case is smaller than the skull from East Runton, and nearly of the same size as the holotype.   The sutures are open, giving evidence that it belonged to a young animal.

The correlation between the antlers, the brain cases and the teeth is made possible by comparison with the holotype.   Two incomplete lower jaws from East Runton
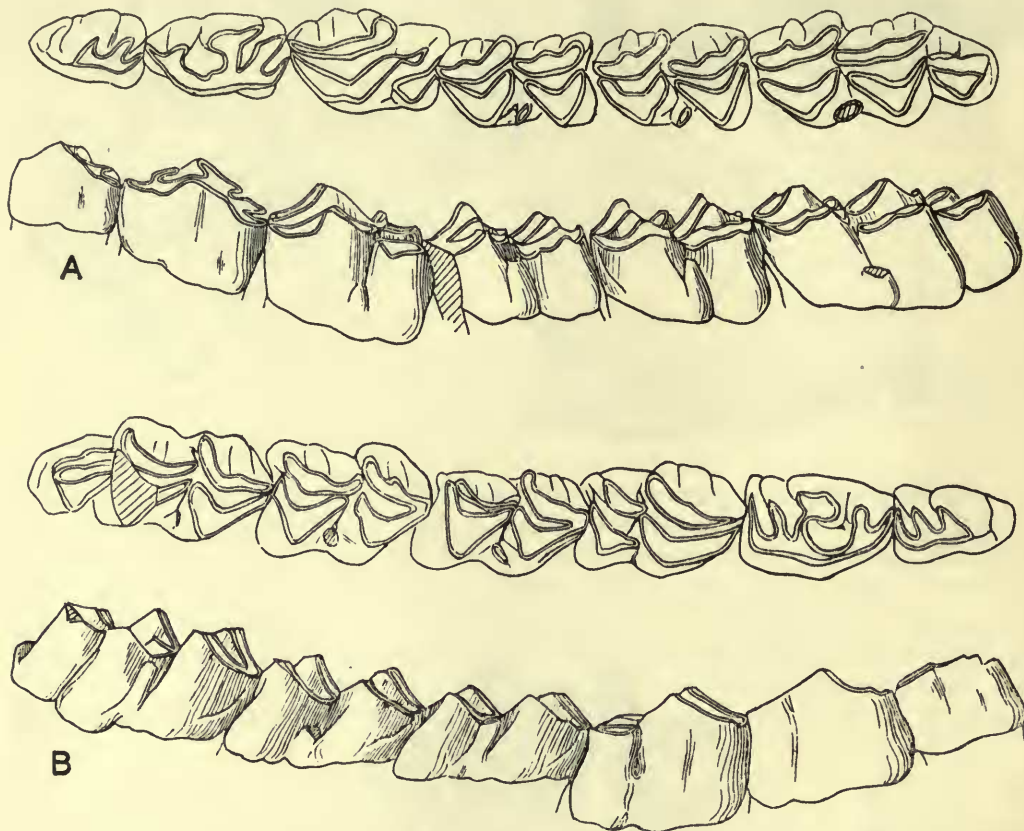
FIG. 4.   A. *Libralces minor*, holotype. Lower dentition, no locality. B.M. (G.D.), M. 6227.   B. *L. gallicus*, lower dentition, East Runton. B.M. (G.D.), M. 6206. Natural size.

(Figs. 4 B, 10 D; Azzaroli, 1952, pl. 15, figs. 3, 4) and some isolated lower molars from Sidestrand may be attributed to this species.

A fine lower jaw in the private collection of Mr. J. E. Sainty of West Runton, recorded also above (section " Geology "), was extracted *in situ* from the Weybourn Crag between East Runton and West Runton.

The identification of more imperfect specimens from other localities will be discussed later.

MEASUREMENTS:—

	E. Runton. B.M. (G.D.) M. 6101		Dogger Bank. B.M. (G.D.) 46108
Skull :			
Occipital breadth . .	164	.	145
Occipital height . . .	107	.	99
Minimal frontal breadth *ca.* .	212	.	
Breadth of condyles . .	82	.	69
Parietal breadth behind the pedicles . . .	109	.	105

	E. Runton B.M. (G.D.) M. 6206
Lower tooth-row :	
Total length	136
Length of the three molars .	80
Breadth of M_2	19

Libralces reynoldsi n. sp.

(Figs. 5 B, 6–8, 9 C.)

1891. *Alces* sp., Gunn, pl. 5, fig. 4.
1934. *Alces latifrons* (Johnson) : Reynolds (pars), fig. 6c.

HOLOTYPE.   B.M. (G.D.) M. 6553: a nearly complete brain case, with the left beam (Figs. 6, 9) figured also by Reynolds, 1933, fig. 6c.   Mundesley.

ADDITIONAL SPECIMENS.   In the British Museum: two very imperfect antlers, from Sidestrand and Mundesley; an imperfect humerus from Overstrand; a naviculocuboid from Overstrand; two phalanges, from Mundesley and Trimingham; a fragment of a lower jaw from Overstrand.   In the Norwich Museum: a lower jaw, from Cromer; two imperfect antlers, the one from Trimingham (Gunn, 1891, pl. 5, fig. 4), the second dredged off the Norfolk coast.

DIAGNOSIS.   A much larger species of *Libralces* than *L. gallicus*, remarkably exceeding also the size of *Cervalces scotti*.   Skull and antlers more heavily built and relatively broader than in *L. gallicus*; other characters closely similar.

DESCRIPTION.   *Libralces reynoldsi* differs from *L. gallicus* in its much larger size, and in some features obviously correlated with this character.   The skull is similarly broad and depressed, and is distinguished by the stronger development of the supraoccipital and supratemporal crests; the latter have developed a distinct knob behind each pedicle.   A close comparison between the skulls of *L. reynoldsi* and of *L. gallicus* shows that their proportions are not identical.   The skull of the larger species is relatively broader: it exceeds that of the genotype by roughly $\frac{1}{4}$ in length and height, and by $\frac{1}{3}$ in breadth.   The holotype of *L. reynoldsi* seems to have been an unusually large specimen; the diameter of its beam above the burr is 96 mm.   In comparison with the strongest specimen of *L. gallicus* from East Runton (52 mm.), this gives a cross-section three times as large.   Apart from the strong development of the supraoccipital crest, no external features intended to counteract the weight of the antlers are seen in the skull, but the thickness of the

frontals, which are massive, measures 40 mm., exactly double that in the larger specimens of *L. gallicus*. The brain cavity is therefore remarkably small. In the holotype it is partly filled with the matrix, a hard sandstone impregnated with iron oxides.
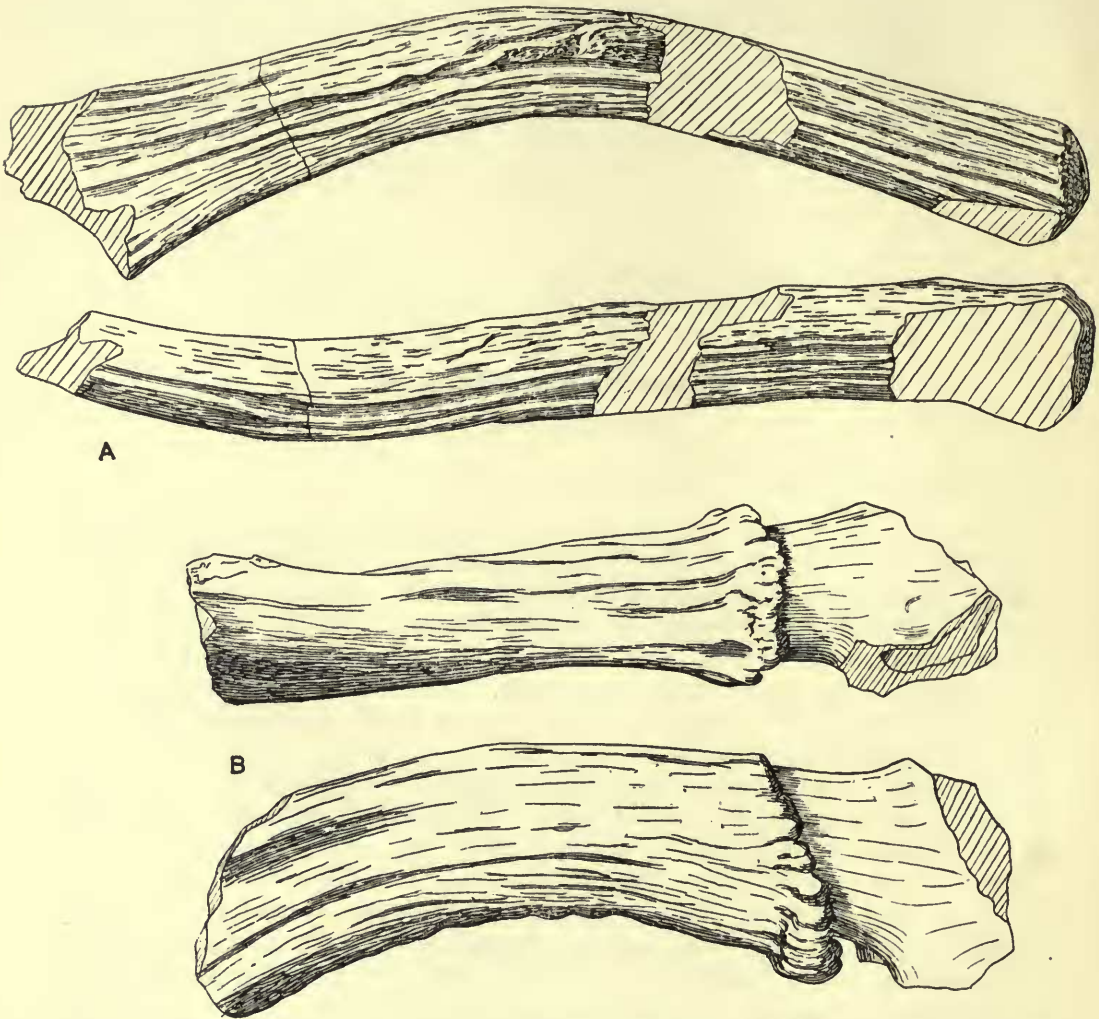
FIG. 5. A. *Libralces gallicus*, right antler from East Runton. B.M. (G.D.), M. 6554. B. *L. reynoldsi*, right antler from Mundesley. B.M. (G.D.), Savin 2223. ¼ natural size.

The remains of the antlers are very incomplete. Unless too much worn, they show a very strong burr and a deeply grooved surface; the beam is gently bent. In the holotype and in the antler of Fig. 5 B, which are the largest specimens I know and presumably belong to the same individual, the beam is short and the

Fig. 6. *Libralces reynoldsi* holotype, Mundesley. B.M. (G.D.), M. 6553. A, front view ; B, upper view ; C, lateral view (the pedicle has b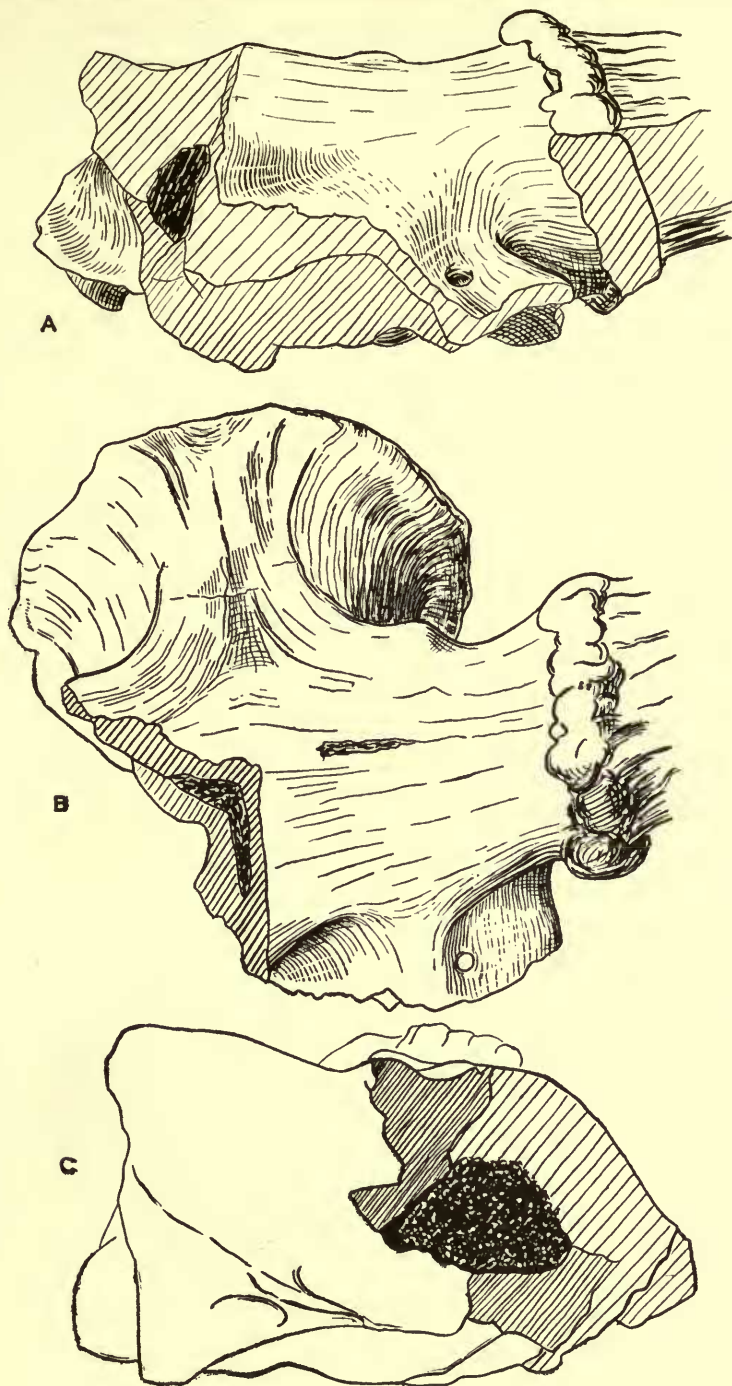een broken off and the anterior part of the brain cavity is exposed). $\frac{1}{3}$ natural size. (Specimen figured by Reynolds, 1933, fig. 6c).

flattening of the palmation is distinctly felt at 25 cm. from the burr. The fragments from Sidestrand and from the Norfolk coast are nearly of the same size, but very incomplete. The smaller antler, from Trimingham (Gunn, 1891, pl. 5, fig. 4), has a diameter of 70 mm. above the burr, and shows that the more slender specimens tended to develop a long beam, as in *L. gallicus*: the flattening is not felt until 35–40 cm. from the burr.

The palmation is not preserved among the fossils of East Anglia, but fairly complete antlers, very probably of this species, have been found in Germany (see below). A maximal span of m. 2·50 has been recorded.

The identification of other specimens is made possible by their size.

It may be safely assumed that the muzzle of *Libralces* displayed the same positive allometry as the other ruminants. We can expect therefore that the difference in size between the teeth of *L. gallicus* and those of *L. reynoldsi* is greater than between their brain cases. No doubt such a comparison is valid only between broad limits, as it has to allow for individual and sexual variations, but it can be used here, where the species under consideration differ very greatly in size. Only two imperfect lower jaws, from Cromer and from Overstrand (Fig. 7), can be attributed to *L. reynoldsi*. Their size exceeds that of *L. gallicus* by roughly ½. The teeth are brachyodont, and display all the characteristic features of *Libralces*.

A humerus showing the characters of the *Alcinae* (Fig. 8), evidently belongs to this species. The proximal epiphysis and half of the distal epiphysis are missing, but from the remaining part a total length of 445–450 mm. can be inferred. A naviculocuboid (Fig. 8) and two phalanges may also be attributed to this species. The naviculocuboid is very large and massive, and relatively higher than the corresponding bone of the giant deer. The three cuneiforms are fused with it. The phalanges are long and slender as in *Alces*, but much larger.

OTHER LOCALITIES. Several remains from Eastern and Central Europe, attributed to *Alces latifrons* by authors, very probably have to be identified with *L. reynoldsi*. Pavlow (1906: 7, pl. 1, figs. 1, 2) described an incomplete antler and a lower jaw from Tiraspol (Bessarabia). The teeth, although much worn, show the same size and characters as those of *L. reynoldsi*. The antler is intermediate in size between the antlers from Mundesley and that from Trimingham, and its beam is relatively long; this seems to confirm the inference drawn from the English specimens that more slender individuals tend to develop longer beams. Another lower jaw with the same characters has been figured by Soergel (1923, pl. 2, figs. 5, 6). It was found in the sands at Mauer, together with other teeth and limb bones, among them a metatarsal of 450 mm. total length. This, too, fits very well with the size of the humerus from Overstrand. The same author stated (1913, 1923) that an " *Alces latifrons* " of nearly the same size is rather common at Mosbach, whereas at Süssenborn an " *Alces latifrons* " of a still larger size has been found. But it is hard to imagine how an animal of this structure could have developed a size still larger than that of our species. Possibly Soergel's statement was based on comparisons between the antlers. According to Vaufrey (1931: 538) more specimens of "*Alces latifrons*" have been found recently at Mosbach. The skull reproduced in his fig. 5, although too much reduced to permit exact comparisons, seems to belong
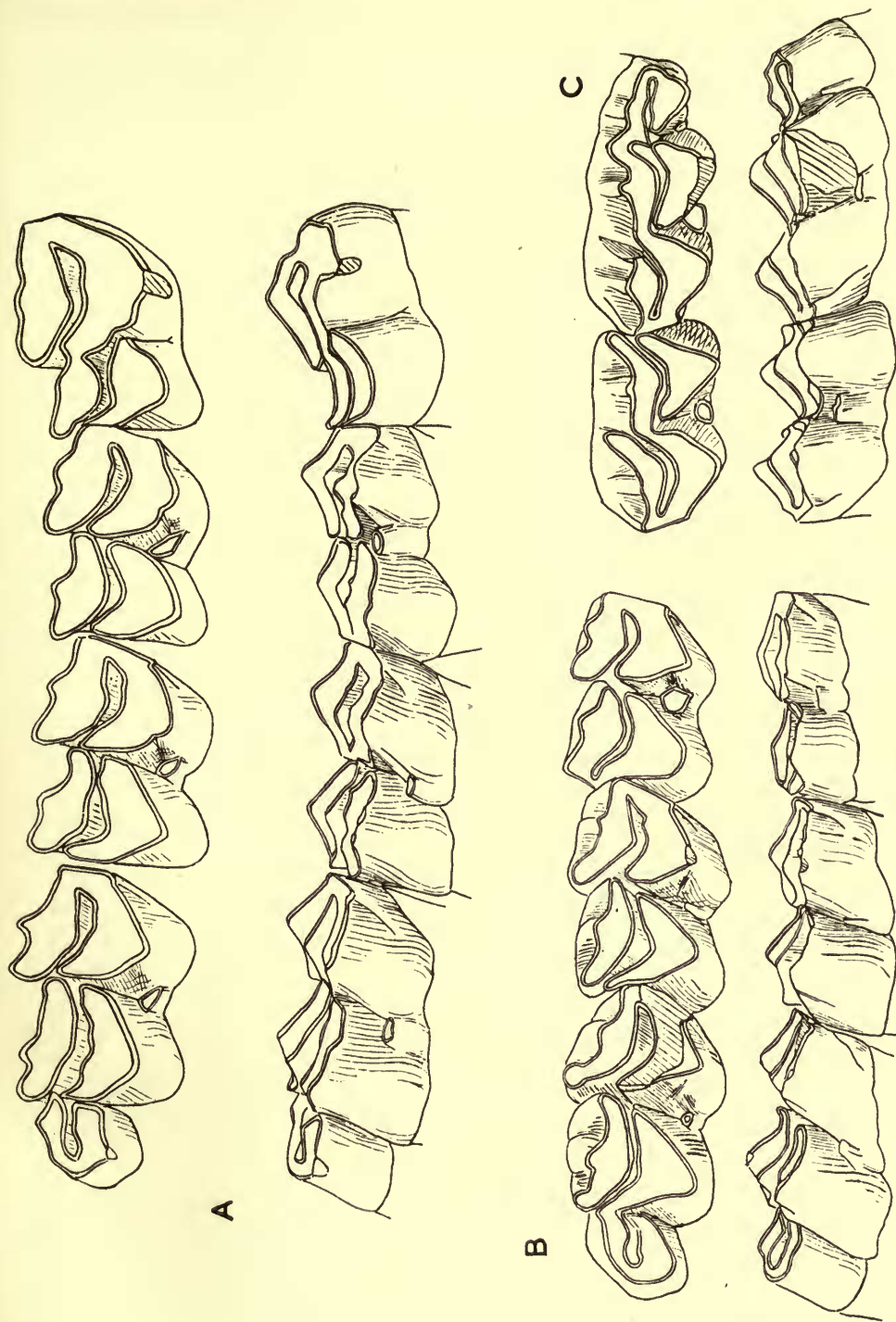
Fig. 7. A. *Libralces reynoldsi*, lower dentition, Cromer. Norwich Museum. 2.116.22. B. *L. cf. reynoldsi*, Lower molars, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1562. C. *L. reynoldsi*, lower molars, Overstrand. B.M. (G.D.), M. 6209. Natural size.

to *L. reynoldsi*. This author recorded a maximal span of m. 2·50 among the fossils from Mosbach.

Recently I have seen a fine lower jaw from Mosbach in the Museum of Natural History at Basel (D. 228), which in all its characters is identical with those of *L. reynoldsi* from the Forest Bed.
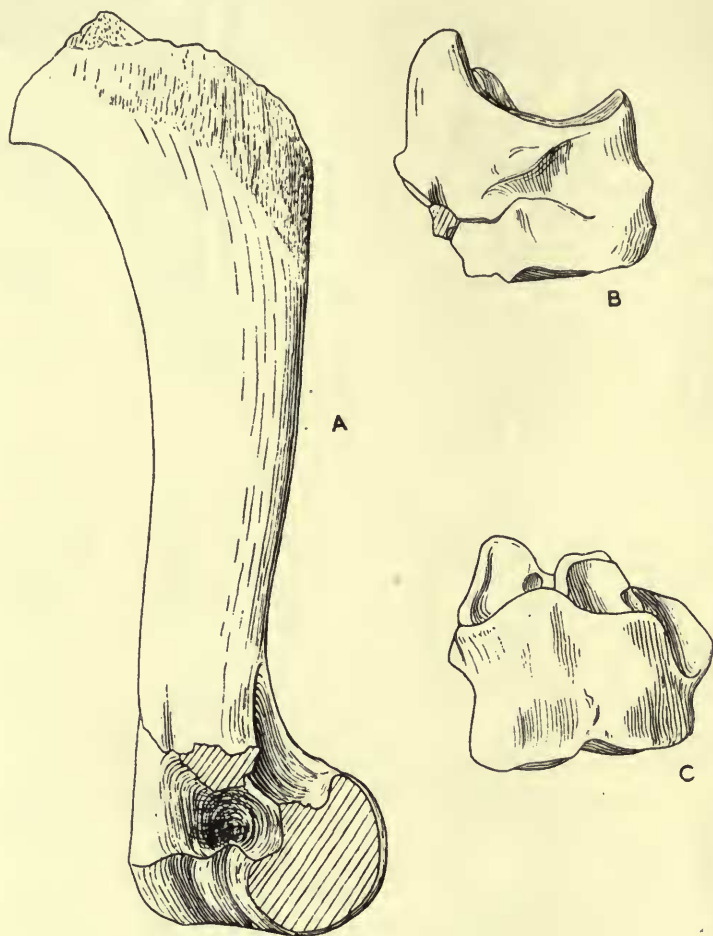
FIG. 8. A. *Libralces reynoldsi*, right humerus, Cromer. B.M. (G.D.), M. 6464. ⅓ natural size. B & C. *L. reynoldsi*, left naviculocuboid, Overstrand. B.M. (G.D.), M. 6526. ⁴⁄₉ natural size.

THE RELATIONSHIPS OF *Libralces reynoldsi*. Although the record of *L. reynoldsi* is not fully satisfactory, its affinities with *L. gallicus* are clearly seen. It is highly probable that *L. reynoldsi* is its direct descendant. These two species differ mainly in size, and increase in size is a common evolutionary trend among ungulates. The antlers of *L. reynoldsi* seem to have evolved following a trend already hinted in

FIG. 9.   Comparison of brain cases.   A. *Alces alces*, male, Norway.   B. *Libralces gallicus*, East Runton.   B.M. (G.D.), M. 6101.   Outline partly reconstructed.   C. *L. reynoldsi*, holotype, Mundesley.   B.M. (G.D.), M. 6553.   Outline partly reconstructed.   About $\frac{1}{5}$ natural size.

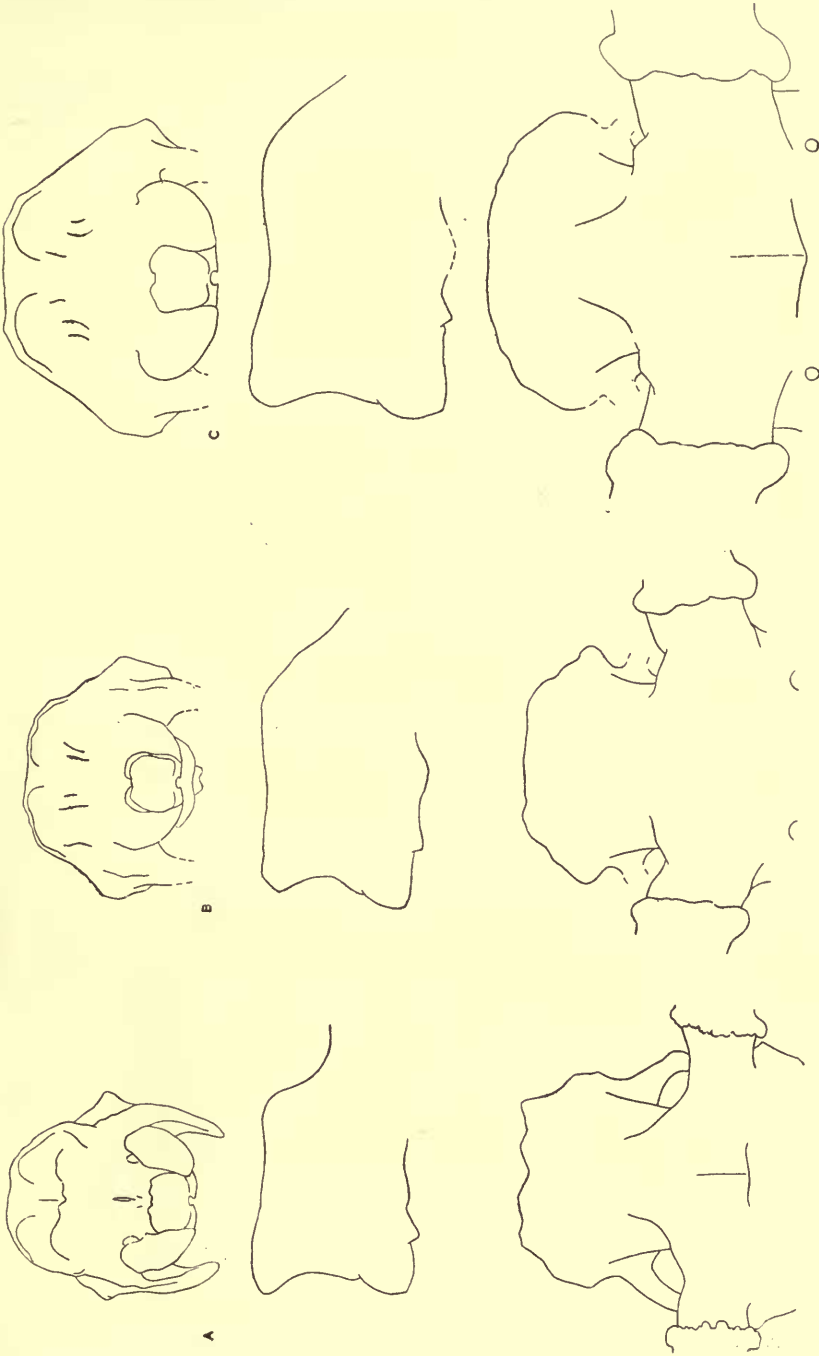*L. gallicus,* that is, increase in size together with a shortening of the beam.   Other differences in the skull, as shown above, are evidently correlated with the increase in weight of the antlers.

L. reynoldsi is distinctly larger than *Cervalces scotti,* and is the largest cervid so far known.   It may be inferred that it stood m. 1·90 to m. 2·00 at the withers; its skull was very heavily built, but its limb bones were long and slender as in the other *Alcinae.*

MEASUREMENTS:—

Skull of the holotype :

Occipital breadth	218
Occipital height	135
Minimal frontal breadth	278
Breadth of the brain case behind the pedicles .	171
Breadth of the condyles	132

Lower tooth row (Cromer, Norwich Museum. 2.116.22)

Length of the three molars	112
Breadth of M_2	25

Humerus (Overstrand, B.M. (G.D.) M. 6462)

Total length	445–450 (inferred)

First anterior phalanx (Mundesley, B.M. (G.D.) M. 6538)

Total length	100
Proximal breadth	42

First posterior phalanx (Trimingham, B.M. (G.D.) M. 6535)

Total length	101
Proximal breadth	38

Naviculocuboid (Overstrand, B.M. (G.D.) M. 6526)

Antero-posterior diameter	75
Transverse diameter	80
Height	42

Libralces cf. *reynoldsi*

From the Upper Freshwater Bed, West Runton.

(Fig. 7 B.)

A fragment of a lower jaw with the three molars, from the Upper Freshwater Bed at West Runton, is distinguished by the very poor development of the basal

columns.   The groove on the anterior crescent of M_1 is well marked; a shallow groove is present also on the anterior crescents of M_2 and M_3.

Libralces minor n. sp.

(Figs. 4 A;   10 A, E, F.)

1934. *Alces latifrons* (Johnson): Reynolds (pars), fig. 6a ?, 7.

HOLOTYPE.   A left lower jaw (B.M. (G.D.) M. 6227.   No exact locality).   Figs. 4 A, 10 A, 10 F.

ADDITIONAL SPECIMENS.   Five incomplete lower jaws (one figured by Reynolds, fig. 7), and a lower molar, from East Runton and Sidestrand.

Possibly some fragments of antlers of a rather small size, from East Runton. The most complete of these fragments was figured by Reynolds, fig. 6a.   Very doubtful specimens come from West Runton, Overstrand and Trimingham.   (See also below.)

DIAGNOSIS.   A *Libralces* with teeth smaller and distinctly narrower than those of *L. gallicus*.

DESCRIPTION.   The teeth need no particular description.   Apart from the smaller size and narrower form, they correspond in all respects to those of *L. gallicus*. The groove on the anterior crescent of M_1 is always clearly seen; it is not very clear in Reynold's photograph, which seems to have been retouched.   A similar groove in M_2 is present in three specimens.   The cross-section of the mandibular ramus is also distinctly narrower than in *L. gallicus* (Fig. 10).

The identification of the antlers is based on their size and is uncertain; it cannot be excluded that the specimens tentatively attributed to *L. gallicus* are young individuals of other species.   The antler figured by Reynolds differs from those of *L. gallicus* in its smaller size, its much shorter beam and its relatively larger palmation. The other specimens from East Runton show the same characters but are still less complete.   One of them (B.M. (G.D.) M. 6550), in Savin's opinion (note in the manuscript catalogue) is possibly the symmetrical part of Reynolds' specimen.

The fragments of beams from Overstrand, Trimingham and West Runton are very imperfect and much worn.

MEASUREMENTS:—

	Holotype. B.M. (G.D.) M. 6227	East Runton. B.M. (G.D.) M. 6210
Lower tooth-row :		
Total length	128	125
Length of the three molars . .	74	71
Breadth of M_2	14	15

Libralces latifrons (Johnson)

(Figs. 10 B, C;   11)

1874. *Cervus latifrons* Johnson, pl. 1.
1887. *Alces latifrons* (Johnson) Dawkins (pars), pl. 1, fig. 6.

HOLOTYPE. A left antler from Happisburgh (Norwich Museum).

ADDITIONAL SPECIMENS. None surely identified, but possibly three lower jaws, from the Forest Bed of Mundesley (Figs. 10, 11), Walcott (Norwich Museum), and Cromer (private collection of J. E. Sainty). For more doubtful specimens see also later.
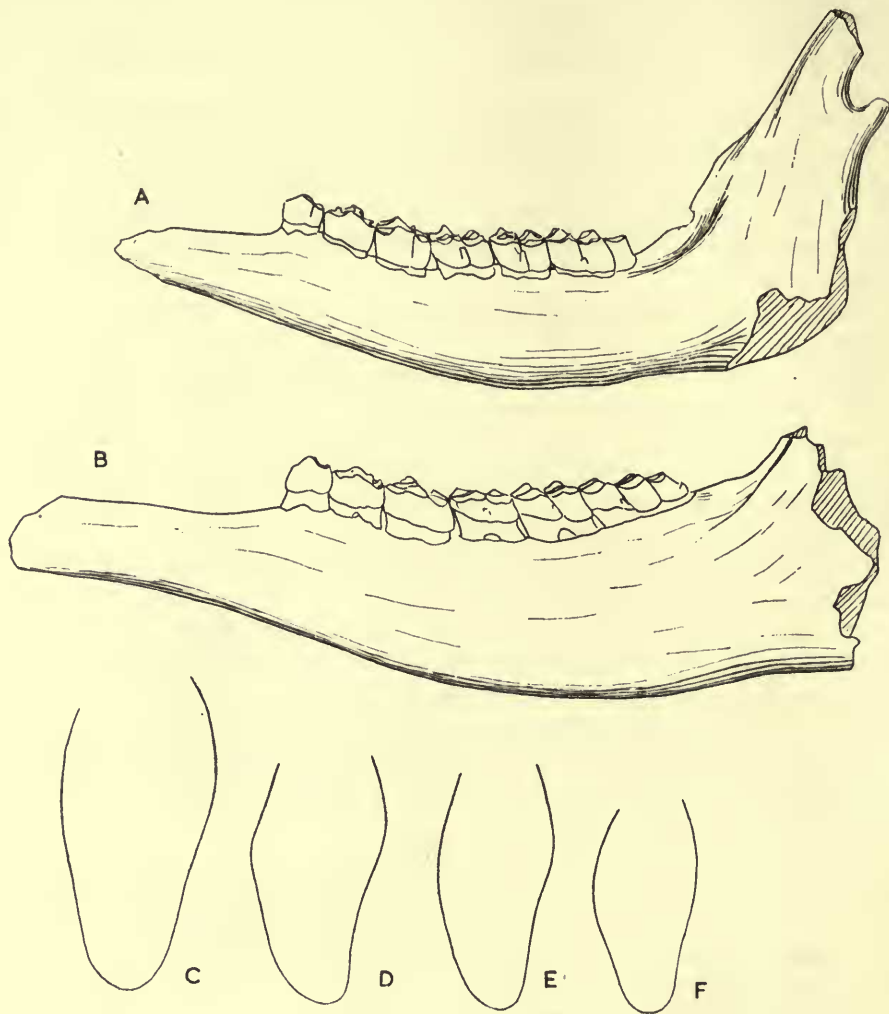

FIG. 10. A. *Libralces minor*, holotype. B.M. (G.D.), M. 6227. ⅓ natural size. (See also Fig. 4.) B. *L. latifrons?* Lower jaw from Mundesley. B.M. (G.D.), Savin 168. ⅓ natural size. C–F. Cross-sections of lower jaws below the hinder lobus of M2. ⅔ natural size. C. *L. latifrons?* B.M. (G.D.), Savin 168. D. *L. gallicus*, East Runton. B.M. (G.D.), M. 6229. E. *L. minor*, East Runton. B.M. (G.D.), M. 6210. (Specimen figured also by Reynolds, 1933, fig. 7.) F. *L. minor*, holotype. B.M. (G.D.), M. 6227.

DESCRIPTION.   This species is based on an incomplete left antler with a part of the frontal, and is ill defined.   The pedicle is long and set horizontally, and the frontal is very thick, as in the other species of *Libralces*.   The size is intermediate between those of *L. gallicus* and of *L. reynoldsi*.   The antler differs from these species in having a short and straight beam; the palmation seems to have been very broad.   The remaining portion of the frontal gives evidence of a larger animal than *L. gallicus*; on the other hand, the shortness of the beam makes it improbable that this fragment belonged to a young specimen of *L. reynoldsi*, but this evidence is by no means conclusive.

In the collections I have seen there are also three lower jaws of a size intermediate between that of *L. gallicus* and that of *L. reynoldsi*.   *L. latifrons* is the only species
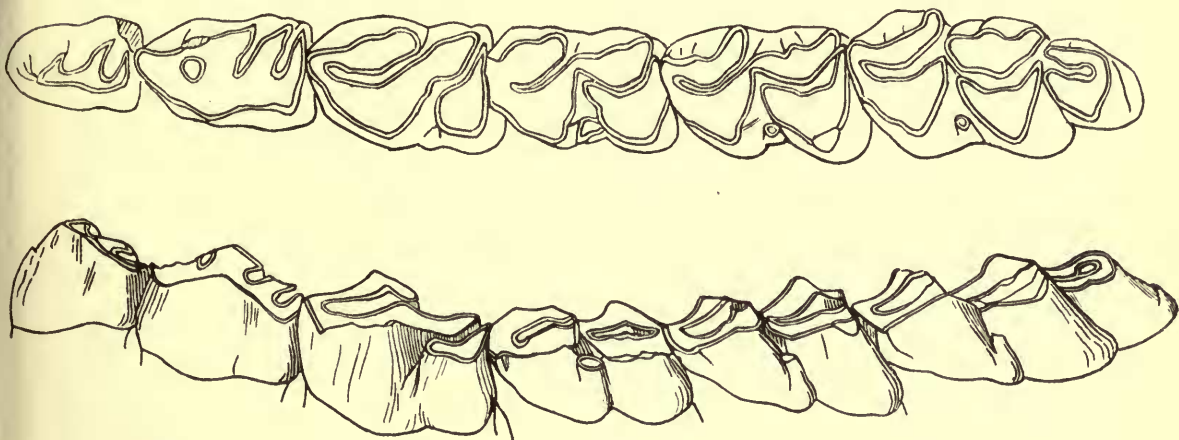

FIG. 11.   *Libralces latifrons?* Lower dentition, Mundesley. B.M. (G.D.), Savin 168.
Natural size.   (See also Fig. 10.)

with which I can tentatively identify them.   The jaw from Mundesley (Figs. 10, 11) is fairly complete.   Its cross-section is remarkably narrow and deep.   There is a distinct burr behind the third lobe of M_3.   A jaw from Walcott (Norwich Museum) and one found on the beach between Cromer and the Runtons (private collection of J. E. Sainty) are more imperfect.

MEASUREMENTS:—

	Mundesley. B.M. (G.D.) Savin 168
Lower tooth-row :	
Total length	151
Length of the three molars . .	88
Breadth of M_2	20

Libralces incertae sedis

(Figs. 12 A, B, C.)

As stated above, the distinction between the four species of *Libralces* is based mainly on the size. Many fragments therefore cannot be identified with certainty; in some instances it is practically impossible to distinguish the smaller species from young individuals of the larger species. A brief account of the most interesting fragments will be given here.

The fragments figured by Dawkins (1887, pl. 1, figs. 2, 3), both much worn, may possibly belong to *L. gallicus*. His pl. 1, fig. 4 is either *L. latifrons* or, more probably, *L. reynoldsi*. Gunn's type of *Alces bovides* (1891, pl. 1 A) may be either *L. gallicus* or *L. minor*. On his plate 5 Gunn figured many specimens attributed to *Alces bovides* and *Alces* sp. The specimen of fig. 5, much rolled, seems to belong to a small species; fig. 1 is the specimen figured by Dawkins on his pl. 1, fig. 2; fig. 2 is neither *Alces* nor *Libralces*; fig. 3 is *Libralces gallicus* (Dawkins' pl. 1, fig. 5), and fig. 4 is *L. reynoldsi* (see above).

The fragment figured by Reynolds, 1933, fig. 6*b*, is very doubtful, and might possibly belong to *Euctenoceros*.

Among the hitherto undescribed specimens, the following are the most interesting:

Fig. 12 A: A fragment of a frontal with the base of the antler, showing a very strong development of the burr. It belonged to a young specimen, probably *L. gallicus*. The frontal is rather thin (14 mm.).

Fig. 12 B: Another fragment of a frontal, with the base of the antler. The pedicle is very long and the flattening begins near to the burr. This is a young specimen of either *L. latifrons* or *L. reynoldsi*.

B.M. (G.D.) Savin 417.—A skull roof of a young specimen, very probably *L. reynoldsi*, from the Forest Bed at Sidestrand. The median suture is open and forms a median ridge. The supratemporal crests are well developed, the pedicles small, giving evidence that the antlers were not yet fully developed. In consequence, the frontal is very thin. Its thickness is 27 mm. on the median ridge, but on the sides of the ridge it is only 16 mm. and the thickness of the parietal is 11 mm.

Fig. 12 C.—An antler from the Forest Bed at Mundesley evidently belongs to an abnormal specimen. It bears a small anterior tine on its proximal portion and shows an abrupt bending at the middle. The characters of the surface sculpture, which shows very deep and large grooves, makes it probable that this fragment belongs to *Libralces*.

Genus *CAPREOLUS* Hamilton Smith

There is not much to say about this genus. As far as I know, only *Capreolus capreolus* has been recorded from the Middle Pleistocene. According to Soergel (1923) this species is fairly common in Germany. The specimens from Mauer, which are of a larger size than the living species, have been distinguished by this author as *C. capreolus* mut. *prisca*.
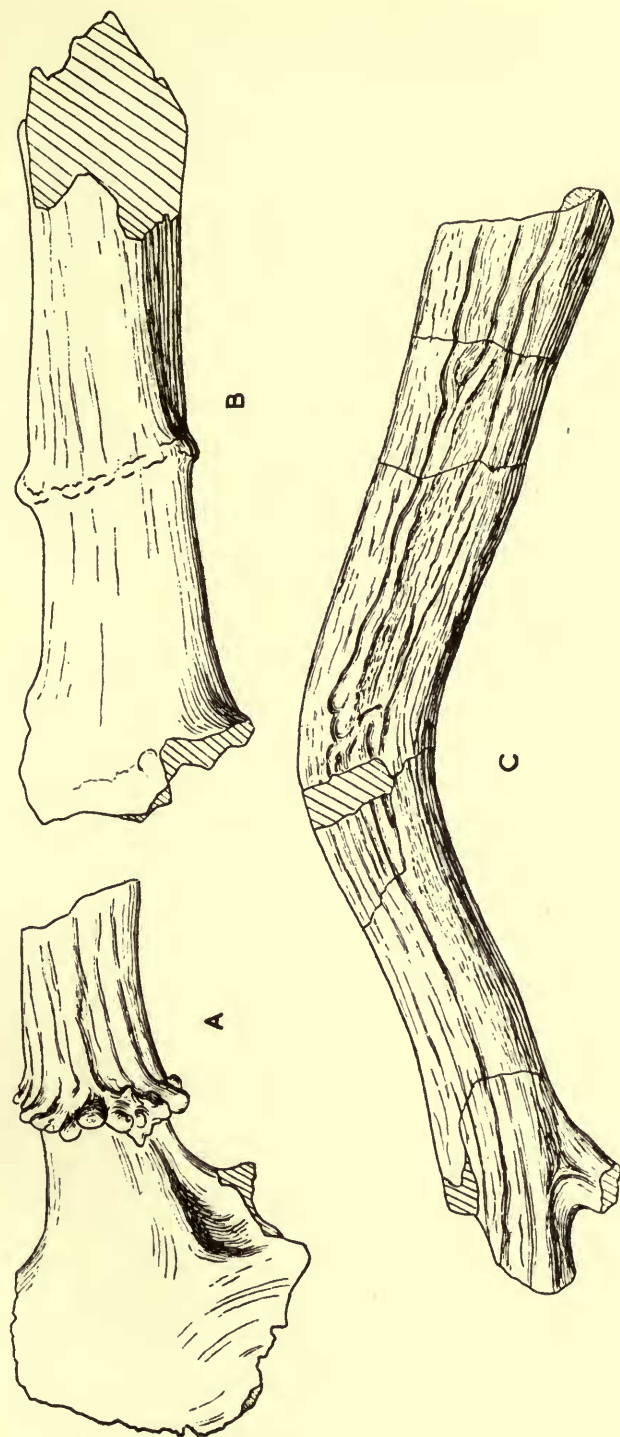
FIG. 12. A. *Libralces gallicus?* Young specimen, no locality, B.M. (G.D.), Savin 749. $\frac{3}{8}$ natural size. B. *L. reynoldsi?* Young specimen from Bacton. B.M. (G.D.), Savin 239. $\frac{3}{8}$ natural size. C. ?*L. gallicus?* Abnormal specimen from Mundesley. B.M. (G.D.), Savin 196. $\frac{1}{4}$ natural size.

Capreolus capreolus (L.)

1882. *Cervus capreolus* L. : Newton, p. 52.
1933. *Cervus capreolus* L. (= *Capreolus caprea* Gray) : Reynolds, p. 34, fig. 15.

DISTRIBUTION. Forest Bed at Overstrand, Ostend, Sidestrand. Doubtful at Happisburgh and Cromer. Upper Freshwater Bed at West Runton.

Newton (1882) questioned the occurrence of the roe in the Forest Bed series. In his opinion a fine antler from Happisburgh (Geol. Survey) may have been found either in the Forest Bed or in the overlying postglacial drift, whereas another specimen from Cromer (Baker coll.) is also of doubtful origin. But Reynolds recorded this species from the Forest Bed of Bacton, Ostend, Overstrand and West Runton (U. Freshwater Bed ?), and figured three fine antlers. In the Savin collection there are in addition a lower jaw from the Forest Bed of Sidestrand and several fragments from the Upper Freshwater Bed of West Runton, namely, two young antlers, three incomplete lower jaws and several isolated incisors and upper molars. There is no reason therefore to question its occurrence in the Forest Bed and Upper Freshwater Bed. The size is somewhat variable, but the material is too scanty for good comparisons.

Genus *CERVUS* L.

The classification of the many species and subspecies of this genus is a thorny problem to palaeontologists. In the very abundant literature many names have been proposed, but the value of a great part of them is questionable. The distinctions have generally been based on antler characters, which may be deceptive owing to the wide range of individual variation. However, they still give the most useful data. The remains of the skull are largely represented by the less significant parts, namely brain cases, lower jaws and teeth. Moreover comparisons with the living species and races are made difficult by the fact that zoologists base their classification mostly on external characters, generally giving little attention to the skulls. However, Pocock's recent studies (1942–43a) on the Indian deer have shown that skulls also may eventually afford valuable data.

A fairly complete account of the species and subspecies of this genus has been given by Lydekker (1915: 116 ff.). He distinguished in the genus *Cervus* seven species; on one of these, *C. albirostris*, Flerow (1930) has founded the genus *Przewalskium*. The remaining six species are: *C. elaphus* L., *C. canadensis* Erxl., *C. yarkandensis* Blanford, *C. wallichi* Cuvier, *C. macneilli* Lydekker, *C. cashmirianus* Gray; the last falls under the synonymy of *C. hanglu* Wagner. They are all characterized by the presence of a bez tine.

C. canadensis, the wapiti, with many varieties ranging from N. America to Central Asia, and *C. macneilli*, ranging over Szechuan, Kansu and Yunnan, are distinguished by the upper tines being placed in a plane parallel to the median plane of the head.

In the other species the upper bifurcations take place transversally to the median plane. *C. wallichi* and its variety *C. wallichi affinis*, the shou (Sikkim and Tibet), are of a very large size. The antlers have generally five tines and end with a simple

transversal fork. An accessory tine seems to occur very rarely. This species has been redescribed recently by Pocock (1942–43*a*), who gave the two varieties full specific rank. *Cervus hanglu*, the hangul, from Kashmir, is a little smaller than *C. wallichi*. Its antlers are similarly built, but an accessory tine or even a double terminal fork are not uncommon (see the good photograph by Stockley, 1948). This species also has been redescribed by Pocock (1942–43*a*). *C. yarkandensis*, from E. Turkestan, has antlers of the same type, generally with five tines, eventually with an accessory tine.

C. elaphus, the familiar red deer, is distinguished by a greater complication of the antlers. As a rule they end with four or more tines forming the characteristic " cup " (" Krone " of the German authors), originated by the fusion of two or more transversal forks (Beninde, 1940). The cup is very variable, especially in some living stocks, which in many ways are influenced by unnatural conditions of life. This, however, does not alter the fundamental fact that the cup is a peculiar feature of *Cervus elaphus*. In the Upper Pleistocene European red deer it is fairly constant.

This species has given origin to many varieties or geographical races; the eastern races are generally larger, but do not attain the size of the wapiti. In the smaller races the antlers are less complicated and the bez tine is sometimes lacking, but the cup, as a rule, is still present.

The typical area of the species is Southern Sweden. Lydekker (1915) listed the following subspecies: *C. elaphus barbarus* Bennett, Algeria and Tunisia; *C. elaphus corsicanus* Erxl., Corsica and Sardinia; *C. elaphus hispanicus* Hilzheimer, S.W. Spain; *C. elaphus atlanticus* Lönnberg, Trondhjem district, Norway; *C. elaphus scoticus* Lönnberg, Scotland; *C. elaphus hippelaphus* Kerr, Germany; *C. elaphus*, unnamed subspecies, Bukovina; *C. elaphus maral* Ogilby, Caucasus and Persia. To these we may add *C. elaphus bolivari* Cabrera, Central and Northern Spain; *C. elaphus brauneri* Charlemagne, Crimea.

The value of some of these subspecies, even as geographical races, is questionable. The craniological studies by Ingebrigtsen (1922–23, 1927) are instructive. According to this author, no distinction is possible between the red deer of Sweden, Germany and the Norwegian mainland districts. Some stocks of the Norwegian isles, especially from Hitra, have developed a smaller size, which is due only to environmental factors and is no expression of hereditary differences. This is true also for the Scottish red deer (see also Ritchie, 1920), and is possibly true for *C. elaphus corsicanus* and *C. elaphus hispanicus*. But two subspecies at least seem to be genetically established: the small *C. elaphus barbarus*, distinguished by its spotted pelage, and the large *C. elaphus maral*, with large but relatively simple antlers and cruciform nasals; this character, as far as I know, has not been recorded in the literature, but is well developed in all the skulls of Caucasian stags exhibited in the British Museum.

No attempt at a complete revision of the fossil red deer will be made here, but it may be useful to give a short account of its earlier representatives.

The red deer has no relatives in the Villafranchian faunas of Central and Western Europe. Redstone (1930) quoted it from the Red Crag, but Dr. K. P. Oakley informs me that the specimen referred to actually came from overlying late Pleisto-

cene deposits. The red deer immigrated from Eastern Europe or from Asia during the Mindel-Riss interglacial, and possibly other immigrations took place later. The best known representatives of the oldest European red deer are not identical with living red deer, and there is no proof of the occurrence of the typical form of *Cervus elaphus* in the Mindel-Riss interglacial.

The most perfect representatives of the genus *Cervus* s. str. were found at Mosbach and Mauer and have been described by Beninde (1937). Further details were added by Haupt (1938), Kleinschmidt (1938) and Schmidtgen (1938).

Cervus acoronatus Beninde, from the sands of Mosbach (main fauna), is a species of large size. It has stout and massive antlers, with five tines, namely, well developed brow and bez tines, a trez tine and a flattened terminal fork, set transversally to the axis of the body. Schmidtgen (1938) has figured an unusually flattened terminal fork, and Kleinschmidt (1938) a terminal fork with a small accessory tine. As a whole, *C. acoronatus* seems to constitute a rather uniform and well characterized stock. The lack of the cup led Beninde to distinguish it from *Cervus elaphus* as a full species. The antlers strikingly recall those of the red deer of Central Asia, especially of the large *C. wallichi*, from which they seem to differ only by the marked flattening of the upper fork and by a stouter form.

Haupt (1938 : 32) proposed to change the name *C. acoronatus* into *C. elaphus mosbachensis*, but this is obviously contrary to the rules of nomenclature. According to Beninde, imperfect antlers of a smaller size occur in the same sands. It is not clear whether they belong to young individuals or to a distinct species.

The deer from Mauer, of nearly the same age if not a little younger, is more poorly represented; it has no typical cup and closely resembles *C. acoronatus*, from which it is distinguished by a twisting of the upper fork, bringing its anterior surface obliquely outwards, and by the presence on it of accessory tines, eventually lying out of its main plane.

Soergel (1923) gave this species the name *C. elaphus* mut. *prisca*, changed into *C. elaphus priscus* by Beninde, but this name is preoccupied. Kleinschmidt (1938a) proposed the name *C. benindei*, and in the same year Haupt proposed *C. elaphus mauerensis*. *C. benindei* has the priority, as it was published in the first months of 1938 (the fascicle was purchased by the British Museum in March), whereas Haupt's paper was published in the second half of the year (see on p. 3 of the same volume the necrology of G. Klemm, who died on 6th August, 1938).

This form is more closely related to *C. acoronatus* than to later red deer; there is no reason therefore to rank it as a subspecies of *C. elaphus* Here it will be called *C. benindei*.

In 1937 Beninde supposed that the upper fork of the red deer from Mauer might represent an intermediate stage, leading to the formation of the cup. This however is not in accordance with his later conclusions (1940) on the origin of the cup, based on comparative studies of recent red deer, that is, that the cup originated through the fusion of two or more transversal forks. The peculiar position of the terminal fork of *C. benindei* does not occur in later red deer. Beninde himself seems to have changed his mind, as he wrote (1940 : 256) : " Im I Interglazial des Oberrheins (Mosbach, Mauer) liegen Geweihe, die gegen den heutigen Rothirsch eine ganz

eigene Stellung einnehmen.   Aber bereits um das Riss (Steinheim a.d. Murr, Primigenius-horizont) erscheinen Hirsche vom rezenten Typus . . . "

The validity of *C. acoronatus* and *C. benindei* has been questioned by Bachofen Echt (1941), who claimed to see intermediate stages between these two species and *C. elaphus* among the fossils from Hundsheim.   However, his observations, which are based on two imperfect specimens, do not invalidate Beninde's conclusions. Moreover the age of Hundsheim, according to Kormos (1937) is " . . .   vielleicht etwas jünger als das Upper Freshwater Bed von West Runton."   If so, it is younger than the main faunas of Mosbach and Mauer.

The remains from the other localities of the same age are scanty and imperfect. They are not identical with the species of Mosbach and Mauer, but do not demonstrate the presence of the true *Cervus elaphus* in the second Interglacial.   The denomination *Cervus* cf. *elaphus* better expresses our state of knowledge.

The red deer from Süssenborn, to which Pohlig (1909) gave the name *C. elaphus trogontherii*, is rather large, and seems to be characterized by the lack of the bez tine.   The status of the red deer in this locality is however not clear.   Some years later Soergel (1923 : 221) quoted *Cervus elaphus* cf. mut. *prisca* Soerg., *Cervus maral fossilis* Ogilby (*sic*), *Cervus* (*Elaphus* n. sp., grosse Form).

A basal portion of an antler from Tiraspol (Pavlow, 1906, pl. 1, fig. 8) is large and stout and bears a strong bez tine.

The red deer from the Upper Valdarno (Azzaroli, 1948) also belongs to this period. It is of a medium size and its antlers are poorly known.

Stehlin (1932) made reference to other early red deer from Jockgrim, Bammental, St. Prest and Solilhac.   The faunas of Solilhac however are not older than the Riss glaciation (Bout & Cailleux, 1951).

The true *Cervus elaphus* is certainly present in the Riss glaciation.   Good specimens from the *Antiquus*-horizon of Steinheim a.d. Murr have been distinguished by Beninde (1937) under the subspecies *C. elaphus angulatus*.   The red deer of the overlying *Primigenius*-horizon is not distinguishable from the typical form.

Cervus cf. *elaphus* L.

(Figs. 13, 14.)

1882. *Cervus elaphus* ? L. : Newton, p. 55.
1891. *Cervus elaphus* L. : Newton, p. 27, pl. 4, fig. 14.
1931. *Cervus elaphus* L. : Reynolds, p. 4.

OCCURRENCE.   This is a very common species in the Forest Bed and in the Upper Freshwater Bed, but its remains are rather poor.   In 1882 Newton questioned the occurrence of the red deer in the Forest Bed, but included it in his faunal list in 1891.   He pointed out that it was then the earliest record of the red deer.   Reynolds recorded it from the Forest Bed at Happisburgh, Overstrand, East Runton and Trimingham.   The specimens I have seen bear the indications : Trimingham, Sidestrand, Bacton, Overstrand, Happisburgh, Mundesley, East Runton (one specimen, much rolled), West Runton (Upper Freshwater Bed), Palling (on the beach).
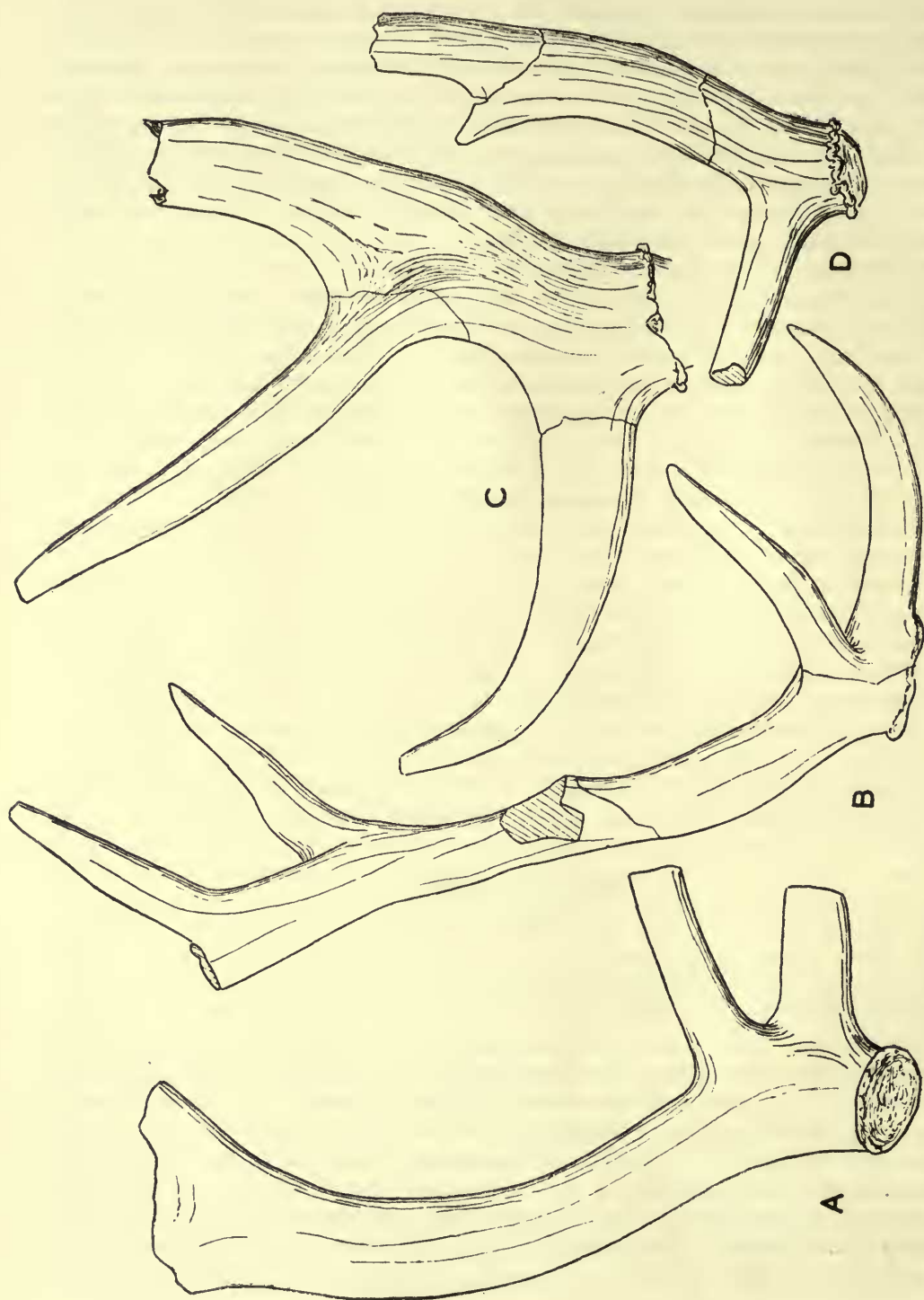
FIG. 13. *Cervus* cf. *elaphus*. Antlers, ¼ natural size. A. Bacton, B.M. (G.D.), Savin 297. B. Trimingham, B.M. (G.D.), Savin 1037. C. Trimingham, B.M. (G.D.), Savin 1349. D. Trimingham, B.M. (G.D.), Savin 1418.

DESCRIPTION. The antlers consist for the most part of basal fragments, and differ greatly in size; some of them are very massive (Fig. 13). The bez tine is generally well developed, and in some instances is pushed upwards. In one young specimen it does not occur in its typical form, but we find here a small tine which may be interpreted indifferently as a bez or a trez (Fig. 13 D). Possibly however some fragments of this species without a bez have escaped my attention.

The only fairly complete antler is of medium size and is very stout. Its upper portion ends with three tines originating from two successive bifurcations, and is damaged. This antler cannot be identified with the species of Mauer and Mosbach, but does not show the typical cup of *C. elaphus*. As it seems to belong to a not fully grown specimen the question of its identity is still open.
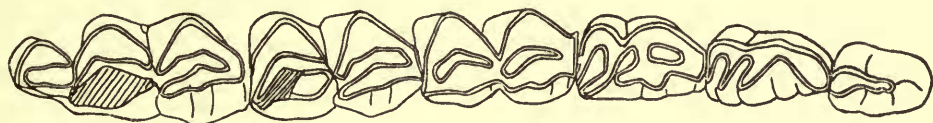

FIG. 14.   *Cervus* cf. *elaphus*, lower dentition, Trimingham.   B.M. (G.D.), M. 6220.   Natural size.

Four lower jaws, from Trimingham and from the Upper Freshwater Bed at W. Runton, do not show any remarkable feature. P_4 is always advanced.

The attribution of some limb bones will be discussed later.

Genus *EUCTENOCEROS* Trouessart

A definition of this genus and a discussion of its synonymy have been given in previous papers (Azzaroli, 1948; Bout & Azzaroli, 1953). In these papers I did not include in it " *Cervus* " *falconeri* Dawk., whose relationships were not clear to me. Kunst (1937) pointed out its affinities to *E. teguliensis* (= *E. ctenoides*; see below), but as a matter of fact these two species differ in many characters. On the contrary its affinities with *E. sedgwicki* are very close. I therefore include it in this genus. It is the oldest and most primitive of its species, but not their common ancestor.

Unfortunately in 1948 I overlooked Nesti's description of the species from the Upper Valdarno, which is not quoted in Forsyth Major's papers and is recorded only in Sherborn's catalogue. Nesti exhibited the deer from the Upper Valdarno at a congress of Italian scientists held in Florence in 1841, and proposed for the larger species the names *Cervus dicranios*, *Cervus ctenoides* and *Cervus orticeros*. His verbal description was summarized in the report of the meeting by the secretaries, Savi & Sismonda (1841). The name *Cervus orticeros* has been subsequently ignored and is probably synonymous with *C. ctenoides*.

These two species have been briefly described also by Cornalia (1858–71: 61). The incorrect spelling *dicranius* has been introduced by Forsyth Major.

The species of this genus display very peculiar features in the antlers, which make

them easily distinguishable from other genera. The first tine branches from the outer anterior part of the beam; the following tines arise from its anterior part and lie in a plane. They are numerous, three in *E. falconeri*, four or five in the other species, and are frequently more or less undulated. Beam and tines display a tendency to become flattened and in some species the tines subdivide further. The flattening is generally more pronounced in the upper portion of the antlers, but in *E. sedgwicki* reaches as far down as the brow tine. In the larger specimens of some species a small accessory tine, directed upwards, is given off from the first bifurcation.

With the sole exception of *E. falconeri* all the species of this genus are of a large size. Together with the common features described above, they display a remarkably wide range of variation which makes specific distinctions difficult. I do not feel satisfied with some of the determinations I published in 1948. An antler from Olivola (fig. 8) then attributed to *E. ctenoides* is actually of *E. dicranios*. The tines of this specimen do not show the strong backward bending of the lectotype, but in its general characters this antler is more similar to it than to *E. ctenoides*. Moreover, my reconstruction was wrong: the lower tine preserved in this antler corresponds to the second tine, not to the third tine of the lectotype of *E. dicranios*.

E. ctenoides and *E. teguliensis* are very probably identical. The antlers do not afford any good basis for distinction.

Euctenoceros tetraceros (Dawkins)
(Figs. 15, 16, 17 A, B, D.)

1878. *Cervus tetraceros* Dawkins, p. 416, figs. 14, 17.
1891. " *Cervus tetraceros* Mackie " : Newton, p. 32, pl. 4, fig. 2.
1953. *Euctenoceros tetraceros* (Dawk.) : Azzaroli *in* Bout & Azzaroli, p. 43, figs. 1–6.

OCCURRENCE. Fairly common at East Runton, rare at Overstrand.

DESCRIPTION. This species is represented by two fine antlers (Fig. 15) and several fragments. They all agree with the specimens from Peyrolles; one specimen only (Fig. 16) is distinguished by the abnormal inward bending of its brow tine. As at Peyrolles, all the antlers of this species have been naturally shed.

Three lower jaws show the same characters as those from Peyrolles. Probably also a fourth lower jaw with a primitive P_4 belongs to this species.

MEASUREMENTS:—

Lower tooth rows :	East Runton. B.M. (G.D.) M. 6232		East Runton. B.M. (G.D.) M. 6218		East Runton. B.M. (G.D.) M. 6221
Total length . . .	131	.	134	.	133
Breadth of M_2 . . .	16	.	15	.	15

Euctenoceros ctenoides (Nesti)

1841. *Cervus ctenoides* Nesti (in Savi & Sismonda, p. 159).
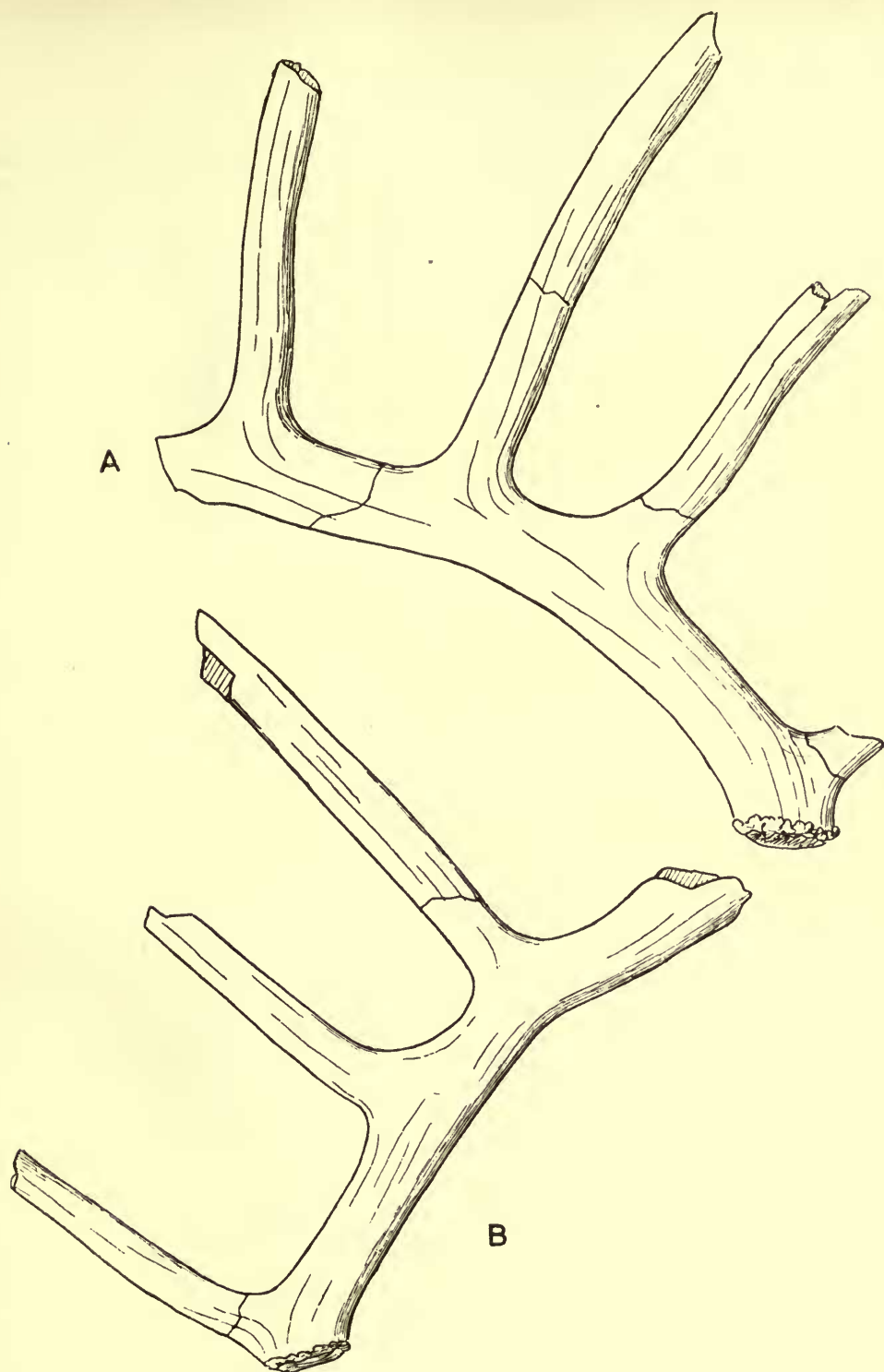1858–71. *Cervus ctenoides* Nesti : Cornalia, p. 61.

FIG. 15. *Euctenoceros tetraceros*, East Runton. $\frac{1}{4}$ natural size. A. Left antler, B.M. (G.D.), M. 6369. B. Right antler, B.M. (G.D.), M. 6370.

1887. *Cervus savini* Dawkins (pars), pl. 3, fig. 4.
1948. *Cervus (Euctenoceros) ctenoides* Nesti : Azzaroli (pars), p. 62, figs. 6, 7, 9.
1947. *Eucladoceros teguliensis* Dub. : Hooijer, p. 34 (cum syn.).

SYNONYMY.   The distinction between *E. ctenoides* and *E. teguliensis* does not seem to be valid.   The ranges of variation of these two species widely overlap. The antlers from Tegelen do not attain the size of the larger specimens from the Upper Valdarno, but this may be due merely to the incompleteness of the record. The dentition and limb bones are of the same size.
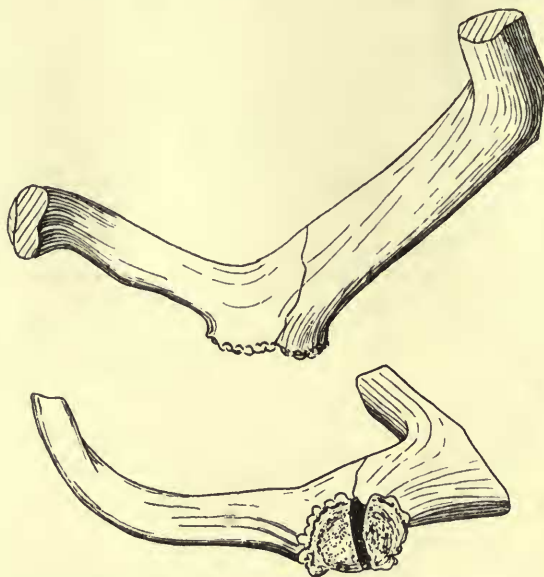

FIG. 16.   *Euctenoceros tetraceros*, abnormal right antler, East Runton.
B.M. (G.D.), M. 6399.   ¼ natural size.

Among the specimens from East Anglia a very fine antler from Sidestrand (Dawkins' pl. 3, fig. 4) so closely resembles the lectotype of *E. ctenoides* that no one would hesitate to identify it with this species.

OCCURRENCE.   The only good evidence of the occurrence of this species is given by the antler from Sidestrand figured by Dawkins, who incorrectly attributed it to *Cervus savini*, and by some basal fragments from East Runton, of a slightly smaller size.

For the identification of other fragments of antlers and of dentitions see later.

Euctenoceros sedgwicki (Falconer)

(Figs. 18, 19, 20 A, 21 A, F.)

1868. *Cervus sedgwicki* Falconer (*ex* Gunn MSS.), p. 472, pl. 37, figs. 1–3.
1882. *Cervus sedgwicki* Falc. : Newton, p. 60.
1891. *Cervus sedgwicki* Falc. : Gunn, pl. 3, figs. 99, 100.
1891. *Cervus* sp. Gunn, pl. 3, figs. 105, 106.
1891. *Cervus sedgwicki* Falconer : Newton, p. 31.

OCCURRENCE. This species is fairly common, but is represented for the most part by very imperfect fragments. The only satisfactory specimen is the holotype (Fig. 18). This and most of the other fragments were found at Bacton, a few specimens at Mundesley and a much rolled fragment at East Runton. For doubtful fragments see also below.
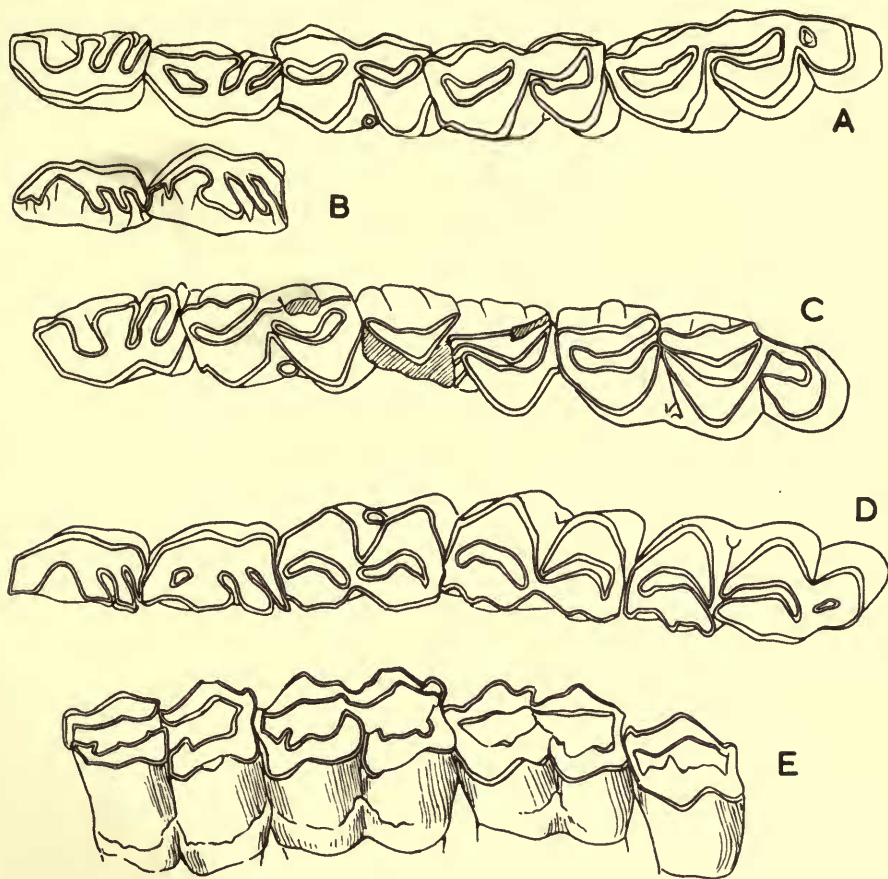

FIG. 17. *Euctenoceros;* dentition, East Runton. Natural size. A. *E. tetraceros*, B.M. (G.D.), M. 6218 (advanced form). B. *E. tetraceros*, B.M. (G.D.), M. 6221 (primitive form). C. *E. ctenoides?* B.M. (G.D.), M. 6241 (primitive form). D. *E. tetraceros*, B.M. (G.D.), M. 6206 (advanced form). E. *E. ctenoides?* B.M. (G.D.), M. 6213.

DESCRIPTION. This species is of a large size and is characterized by the high position of the brow tine, 10–15 cm. above the burr, and by a very marked flattening of the upper portion of the beam and of the tines, which divide into three or four secondary tines. The brow tine is also much flattened, and in the type it divides into four points. The high position and the flattening of the brow tine are remarkably constant, and are well displayed even in young specimens (Fig. 21 F). The pedicles are set near one another, as in *E. boulei* and *E. dicranios.*
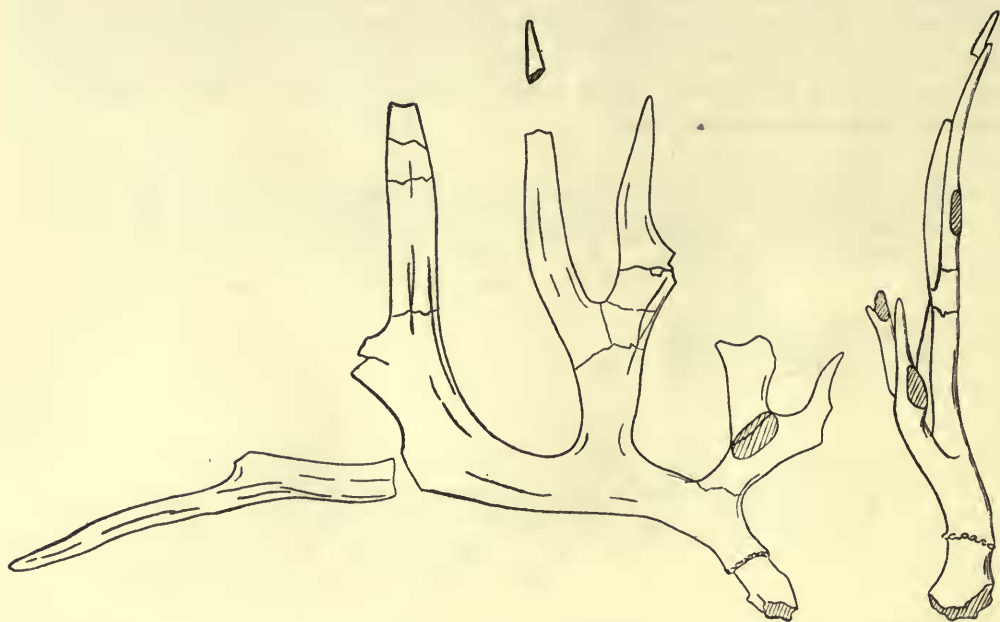
FIG. 18.—*Euctenoceros sedgwicki*, holotype, Norwich Museum, Gunn Colln. No. 99. $\frac{1}{13}$ natural size.
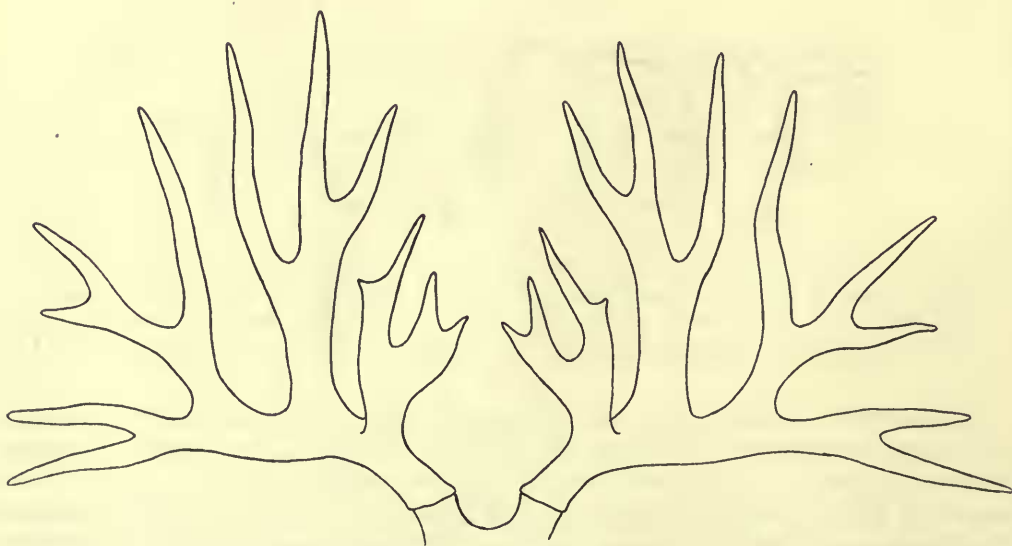

FIG. 19.   *Euctenoceros sedgwicki*, reconstruction of the holotype.   Norwich Museum, Gunn Colln. No. 99. $\frac{1}{8}$ natural size.

The upper portion of the type antler is badly damaged and its reconstruction is rather puzzling. On Fig. 18 I have indicated the most probable position of the fragments. The small cross-section of the beam at the broken surface makes it unlikely that there were additional tines. On Fig. 19 I have attempted a reconstruction of this specimen.

COMPARISONS. *Euctenoceros falconeri* (Dawkins, 1868; see also Kunst, 1937 : 101) is a species of medium size. It does not occur in the Weybourn Crag nor in the Forest Bed, but has been found in the Red Crag and in the Norwich Crag.
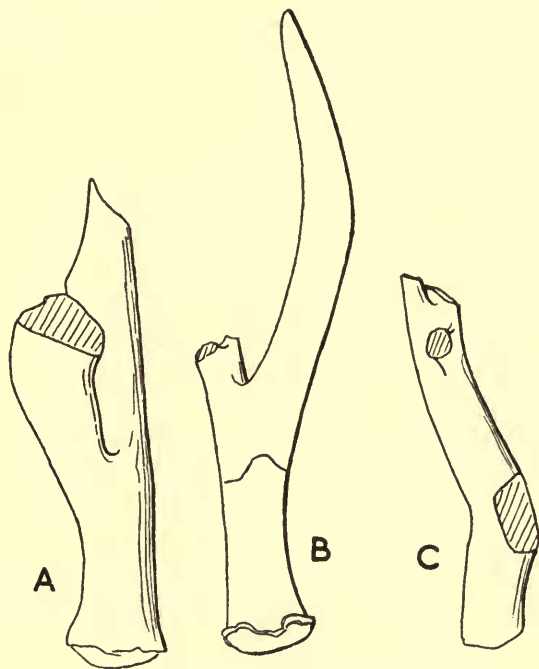

FIG. 20. *Euctenoceros sedgwicki* and *E. falconeri*, lower portions of the antlers. ⅛ natural size. A. *E. sedgwicki*, Mundesley. Norwich Museum 323. B. *E. falconeri*, Thorpe, Norwich Crag. Norwich Museum 313. C. *E. falconeri*, Horstead, Norwich Crag. Norwich Museum 310.

It occurs also in the Poederlian of the Netherlands and in deposits of the same age in Belgium. The most complete specimens were found in the Belgian Kempen. The remains from East Anglia are rather fragmentary; the most complete are the holotype (a young individual), and a crushed full-grown antler from the Red Crag, now in the Museum at Ipswich. In the British Museum and at Norwich I have seen other fragments from the Norwich Crag, and at Ipswich fragments from the Red Crag. The remains of the Norwich Crag may possibly have been derived from the Red Crag. Those from the Red Crag bear no exact indication of the horizon, but their state of fossilization shows that they were not derived.

Two specimens in the Norwich Museum were figured by Gunn (1891, pl. 2, fig.
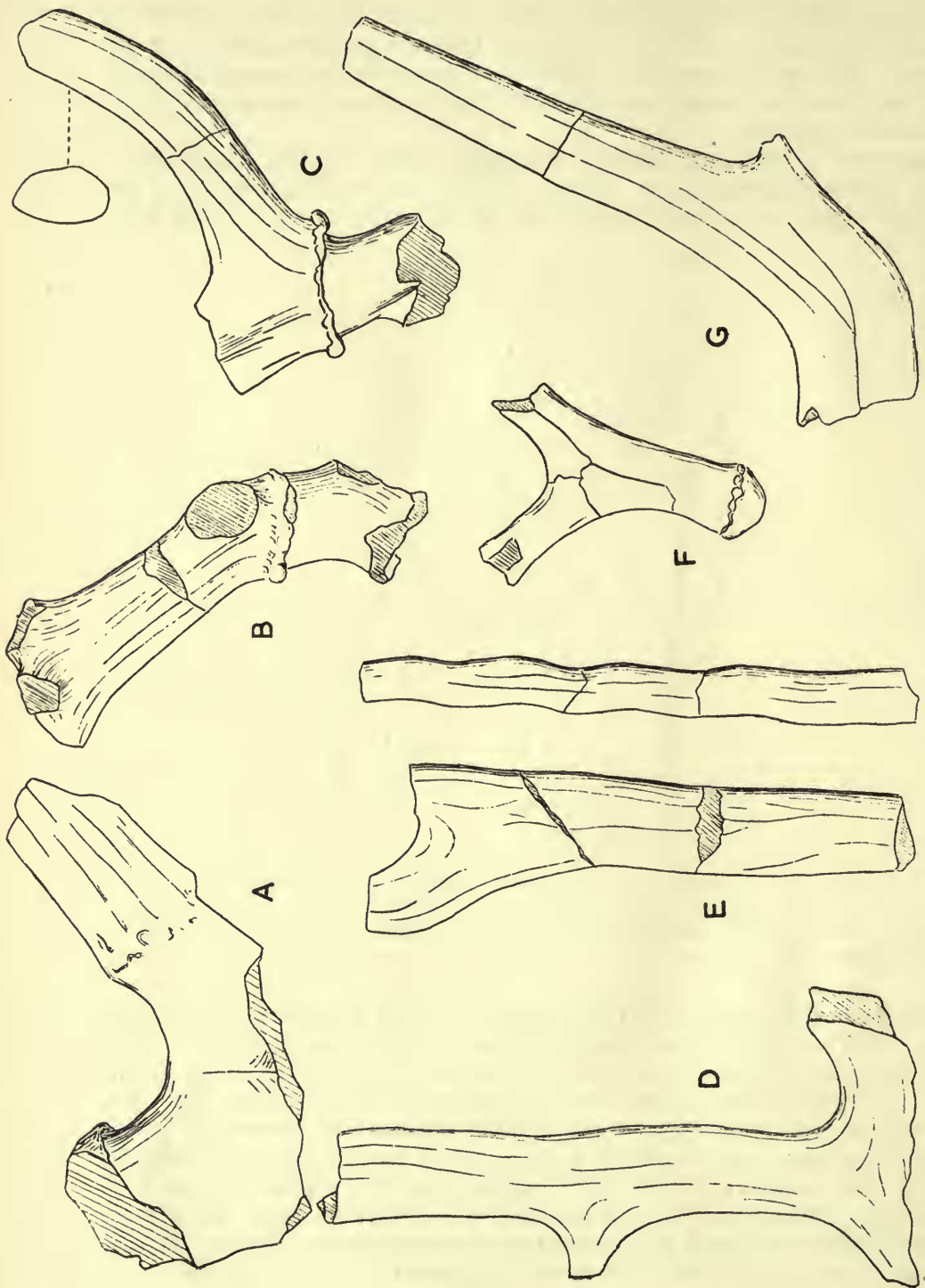
FIG. 21. *Euctenoceros*, fragments of antlers. A. *E. sedgwicki*, frontal and base of an antler from Bacton. B.M. (G.D.), Savin 244. ¼ natural size. B. *E. ctenoides?* Right antler, with abnormal tine on the outer side, front view. Overstrand, B.M. (G.D.), M. 6384. ¼ natural size. C. *E.* sp. Basal portion of a right antler from East Runton. B.M. (G.D.), M. 6387. ¼ natural size. D. *E. ctenoides?* Fragment of an antler from East Runton. B.M. (G.D.), M. 6395. ¼ natural size. E. *E. ctenoides?* Fragment of an antler. B.M. (G.D.), M. 6351. ¼ natural size. F. *E. sedgwicki*, antler of a young specimen, Bacton. B.M. (G.D.), Savin 2206. ¼ natural size. G. *E. ctenoides?* Fragment of the upper portion of an antler. No locality. B.M. (G.D.), Savin 898. ¼ natural size.

97 ; pl. 7, fig. 3), who did not determine them.   Two other specimens of the same species were attributed to *Cervus carnutorum* Laugel and to *Cervus ardeus* Croizet & Jobert by Newton (1891 : 25–26, pl. 4, figs. 3, 6).

The relationships between *E. falconeri* and *E. sedgwicki* are very close.   They are both distinguished by the high position of the first bifurcation and by the well-marked flattening of the upper portion of the antlers.   Very probably *E. sedgwicki* is the descendant of its older ally, from which it is distinguished only by more advanced characters, namely, the larger size, the greater number of the tines and their more pronounced flattening.

The relationships with *E. boulei* (Teilhard & Piveteau, 1930) are also very close. In *E. boulei* the flattening is confined to the upper tines; its range of variation seems to be very wide.

The relationships of *E. sedgwicki* with *E. dicranios* from the Upper Valdarno (Azzaroli, 1948) seem to be less close.   The range of variation of this species is little known ; but it is always distinguished by the low position of the brow tine, by a peculiar backward bending of the upper tines and by their low grade of flattening. The tines of its lectotype are more numerous than in the type of *E. sedgwicki*.

The few specimens from Olivola (see also above, introduction to the genus *Euctenoceros*) do not agree perfectly with those of the Upper Valdarno.   In the more complete skull (Azzaroli, 1948, fig. 10) the first bifurcation is set 8 cm. above the burr, and in the antler (fig. 8, incorrectly determined *E. ctenoides*) the backward bending of the upper tines is less pronounced.   These specimens are probably slightly older than those from the Upper Valdarno (Azzaroli, 1950).   *E. dicranios* may also be a descendant of *E. falconeri*; the question however is still open. The frontal from St. Prest, figured by Gervais (1867–69, pl. 16, fig. 4) and determined as *Cervus (Megaceros) carnutorum* Laugel, might possibly belong to *E. sedgwicki*.   The name *Cervus carnutorum* was based on fragments of different species and should be dropped (Stehlin, 1912).

Euctenoceros, incertae sedis

(Figs. 17 C, E, 21 B–E, G, 22)

Three lower jaws and a maxilla from East Runton and Sidestrand might be attributed indifferently to *E. ctenoides* or *E. sedgwicki*.   *E. sedgwicki* is not otherwise recorded with certainty from these localities.   The teeth are slightly larger, broader and more brachydont than those of *E. tetraceros*; the upper molars bear a discontinuous cingulum.

A large basal fragment of an antler from East Runton is rather puzzling (Fig. 21 C).   It strikingly recalls *E. dicranios* from the Upper Valdarno.

Two bifurcated tines from the same locality (Fig. 21 D, E) might perhaps be attributed to *E. ctenoides* but are very imperfect.

An upper portion of an antler (Fig. 21 G), and two similar fragments, from East Runton and Overstrand, may be attributed indifferently to *E. ctenoides* or to *E. sedgwicki* (cf. the two antlers of *E. ctenoides* in the Museum at Basel, figured by Kunst, 1937 : 42).

An antler from Overstrand (Fig. 21 B), with an abnormal outer tine near the base of the second tine, might also belong to *E. ctenoides*.

A fragment of a frontal with an abnormally reduced antler from East Runton (Fig. 22) affords an example of degeneration, probably due to very old age. The antler is much thinner than the pedicle and is reduced to a forked stump. Among the species from this locality, *E. tetraceros*, is, for its size, the only one to which this fragment might be attributed. Also a skull-roof from the same locality, with shed antlers (B.M. (G.D.), M. 6300), might belong to *E. tetraceros*. This specimen is of little interest. Its supraoccipital crest is weak.

A fragment of an antler attributed to "*Alces latifrons*" by Reynolds (1933, fig. 6*b*) might possibly belong to *E. sedgwicki*.
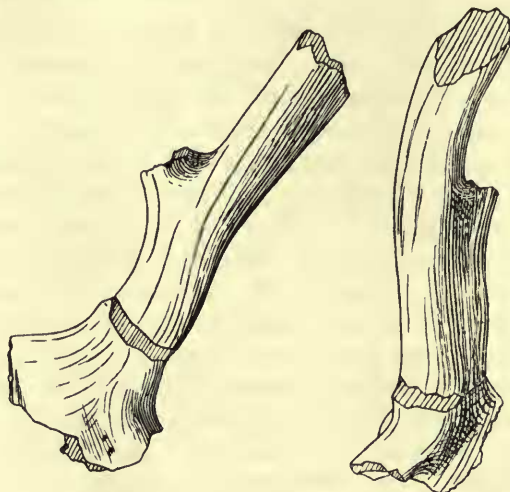
FIG. 22. *Euctenoceros ?* sp. Basal portion of a left antler. Abnormal specimen, presumably very old. East Runton, B.M. (G.D.), Savin 1776. ¼ natural size.

MEASUREMENTS:—

	Sidestrand. B.M. (G.D.) Savin 1615
Lower jaw :	
Total length of the tooth row	141
Breadth of M_2	18

	East Runton. B.M. (G.D.) M. 6300
Skull roof—	
Occipital breadth	135
Occipital height	84
Minimal frontal breadth *ca.*	146
Breadth of condyles	81

Genus *MEGACEROS* Owen

Many species more or less closely related to the familiar giant deer have been described in the last decades. They have generally been united under the name

Megaceros, alternately taken as a full genus or ranked as a subgenus of *Cervus*. Some terminal forms from North Africa and Eastern Asia have been separated under the subgenera *Megaceroides* Lydekker and *Sinomegaceros* Dietrich.

It is easily seen that this group is characterized by peculiar features of the skull, the antlers, the dentition and the limb bones; and although it is a plesiometacarpal, it widely differs from the other *Cervinae*. It is consistent therefore to give it full generic rank.

Megaceros is characterized by its large size, heavy build, large antlers, which generally are more or less palmated, and by a strange hyperostosis of the mandibular ramus and in a lesser degree of the skull, which eventually leads to monstrous forms. The significance of this hyperostosis has puzzled many palaeontologists, who often considered it a mark of degeneration or even a pathological character. However its occurrence in all the species of this genus gives evidence that it is not pathological in the common signification of the word; the more so as in the most widespread species it does not display any particularly wide range of variation. On the other hand it can hardly be considered a useful character, but always has a distinct mark of abnormality. Much light has been thrown on this point by Young's studies on *Megaceros pachyosteus* (1932), a very abundant species from the *Sinanthropus* site at Chouk'outien and other localities of Central China. In this species, which obviously belongs to a terminal branch, the hyperostosis is extreme. At the same time it displays a very wide range of variation, both in degree and in the way it affects the bones, and is accompanied by characteristic marks of degeneration, namely a shortening of the muzzle, small body size with an unusually wide range of variation, and the frequent occurrence of distinctly dwarf individuals. Young came to the conclusion that " . . . in the case of *Cervus pachyosteus* we witness a zoological group in some state of high zoological instability (or ' affolement '), this condition being due to a factor (the hyperostosis) which can be called a morbid one, since it was not directed to the formation of useful features."

Zdansky (1925–27) attributed the hyperostotic bones to various genera, but according to Young these identifications are incorrect.

Similarly degenerate characters (an extreme degree of hyperostosis, a very marked shortening of the muzzle and a small size) are displayed by another terminal form, *M. algericus* Lydekker (in Arambourg, 1938). This hyperostosis, as will be shown later, is well developed even in the earliest representatives of this genus in Europe, and there is no evidence of an increase of it with time.

An attempt to trace the phylogeny of the giant deer was made by Soergel (1927), who ranged the species in a unique phyletic line and assumed that they were derived from a Pliocene or Lower Pleistocene ancestor from N. Italy, *Cervus pliotarandoides* Alessandri. Soergel based his observations mainly on the antlers, and came to the conclusion that their evolution, starting from an hypothetical Pliocene ancestor with two basal tines (which he homologized with the brow and the bez tine of the red deer) was characterized by the disappearance of the lower (brow) tine and by a gradual downwards shift of the upper (bez) tine till close to the burr.

Many data have been made known since, and Soergel's conclusions need revision.

First of all, a strict homologizing with the brow and bez tine of the red deer is not possible. The antlers of *Megaceros* are built on a peculiar plan, very different from that of *Cervus* and the other *Cervinae*. We shall follow here the current nomenclature and refer to the fairly constant basal tine as the brow tine. Some species occasionally develop an inconstant additional tine below it, which will be referred to as the accessory basal tine. Moreover, the chronological sequence is not in accordance with Soergel's views.

The species of giant deer recorded in the literature are very numerous. Many of them, of course, are poorly known and of questionable value, but the better known species can easily be divided into two groups.

The skulls of the older species consist only of more or less complete brain cases. The antlers as a rule vary greatly; both skulls and antlers however give very valuable information on the relationships of the species. The teeth afford good examples of evolutionary progress with time, but seem to have advanced along parallel lines and are therefore of a more restricted use in classification. Moreover, their identification with skulls and antlers is sometimes uncertain.

The limb bones are robust. Young pointed out the broad form of the distal epiphysis of the metapodials in *Megaceros pachyosteus*. This character, although less pronounced than in the reindeer, is quite distinct and seems to occur in all the species of this genus. It has not yet been possible to establish whether limb bones may give some indication for classification.

The two groups into which this genus can be divided will be called, from their best known representatives, the group of *Megaceros giganteus* (= *M. euryceros* Aldrov.; for the priority of the name see Berckhemer, 1941) and the group of *M. verticornis* Dawk. The subgenera *Megaceroides* and *Sinomegaceros* mentioned above probably represent terminal branches of each group, but their relationships with the European species are not known with sufficient detail. Moreover the value of *Sinomegaceros* has been questioned by Teilhard (1936). These two subgeneric names therefore will not be used here.

The Group of Megaceros giganteus

Pedicles divergent, but generally set near one another. Forehead hollowed in front of the pedicles (Fig. 23 D), and eventually swollen into a prominent transverse ridge between them. Brow tine branching off closely near the burr, flattened and more or less expanded, fluctuating in some of the younger species.

To this group I attribute: *Megaceros giganteus* Blumenbach; *M. antecedens* Berckhemer; *M. savini* Dawkins; *M.* sp. from Felixstow, Red Crag, East Anglia; *M. pachyosteus* Young; *M. ordosianus* Young; *M. flabellatus* Young; *M. yabei* Shikama.

Megaceros giganteus is the largest and most advanced species of this group, and is very familiar to palaeontologists. It was very widespread through Europe during the last interglacial and glacial phases. According to Mitchell & Parkes (1949), the Irish race was an inhabitant of grassy lowlands and the period of its maximal spread coincides with a mild Würm Interstadial, corresponding to the Alleröd

stage of Denmark; it seems to have become extinct with the last cold phase.   The races of Central and Southern Europe had presumably the same habits of life.   I have not been able to find satisfactory information on their chronological range, but there is no evidence that any of them outlived the last glaciation (see also Frentzen & Speyer, 1928).
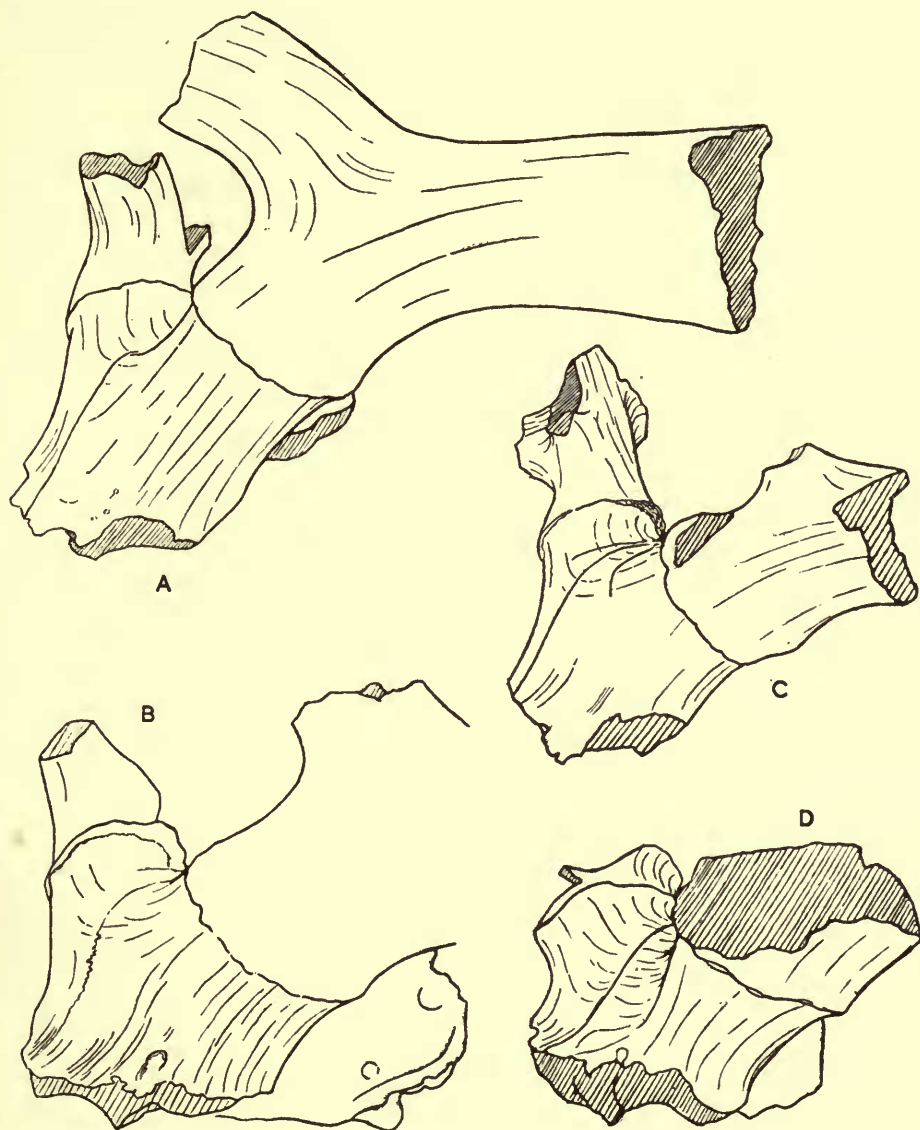

FIG. 23.   Frontals of *Megaceros*, about ⅓ natural size.   A. *M. verticornis*, Pakefield. Norwich Museum 365.   B. *M. verticornis*, Kessingland.   Norwich Museum 364. C. *M. dawkinsi*, Sidestrand, B.M. (G.D.), M. 6302.   (See also Fig. 33A.)   D. *M. savini*, Kessingland.   Norwich Museum 321.

Further references to this species may be found in Cornalia (1858–71), Pohlig (1892), Pavlow (1906), Hescheler (1909), Fabiani (1919), Frentzen & Speyer (1928), Reynolds (1929), Zakrewska (1932, 1935), Kunst (1937), Kirchner (1937), Azzaroli (1948). Pohlig distinguished three races, *hiberniae*, *germaniae* and *italiae*, based on antler characters. This distinction has not been accepted by all authors. Recently Kirchner rejected it, claiming that their ranges of variation widely overlap, but I am unable to accept his views. I grant that the variation is great and that extreme variants may eventually overlap, but on the whole Pohlig's specimens from Germany are quite distinct from the Irish specimens, and the distinctive characters listed by this author hold good, at least in a statistical sense. This is true also for the specimens described by Frentzen & Speyer. In discussing the range of variation of the German race Kirchner made reference to an incomplete antler from Bergrhein-feld a. Main, which actually seems to fit better with the Irish race; but its age is somewhat uncertain, possibly younger than Pohlig's specimens, and it cannot be taken therefore as a good representative of the German race.

The distinction of the Italian race is less clear, owing perhaps also to the incompleteness of the record. The identifications with Pohlig's races, made by some authors for specimens from other districts, are questionable. No doubt more detailed information on the age of the specimens will throw much light on their relationships and on the value of these smaller systematic units.

Megaceros antecedens from the *antiquus*-horizon of Steinheim a.d. Murr (a mild Riss interstadial; Berckhemer, 1941) has been described as a subspecies of *M. giganteus*, but I prefer to give it full specific rank. It is smaller than *M. giganteus* and its dentition is more primitive. The antlers are stout, little divergent and broadly palmated. The brow tine is expanded into a small palmation. A related form, not yet well defined, occurs in the overlying *primigenius*-horizon.

Megaceros savini from the Forest Bed is still more primitive. The brow tine is widely expanded, the beam is long and flattened and ends with three tines. This is the only example of the lack of a palmation in the genus *Megaceros*. The dentition is primitive. A more detailed description will be given later.

Megaceros sp. ind. from the Red Crag at Felixstow is represented by a basal fragment of an antler, described and figured by Owen (1856, fig. 18), and is now in the Museum at Ipswich. It is a very poor fragment. The brow tine is broken; its base lies close to the burr and is slightly expanded, as in *M. giganteus*; the beam shows the same sigmoidal swing. For these reasons I attribute it to this group. There is no certain information about the horizon of this specimen. Its fossilization shows that it was derived possibly from the lower part of the Red Crag.

Megaceros pachyosteus (Young, 1932) was found at the *Sinanthropus* site at Chouk'outien and at other localities of Central China. At Chouk'outien it is extremely abundant. Its skull and antlers clearly show the characters of this group; it is distinguished by a relatively small size, a very brachyodont dentition, an extreme hyperostosis of the skull, and by other characters clearly pointing to degeneration. The skull is very broad and depressed, the muzzle short, the body size is very variable and distinctly dwarf individuals are not uncommon. Also the

antlers are very variable, but are always very stout and broadly palmated.   The brow tine is also palmated.   The dentition is still rather primitive.

Megaceros ordosianus from the loess of Manchuria, *M. flabellatus* from locality 9 at Chouk'outien and *M. yabei* from the Upper Pleistocene of Japan (Young, 1932; Teilhard, 1936; Shikama, 1939) are distinguished from *M. pachyosteus* by a less developed hyperostosis and by some characters of the antlers.   According to Teilhard the wide range of variation makes specific distinctions somewhat difficult.

The Group of Megaceros verticornis

Pedicles divergent, generally set wide apart and directed obliquely backwards. Forehead transversely flat or convex in front of the pedicles (Fig. 23), generally marked by two faint ridges running along the median bases of the pedicles and vanishing on the forehead.   No transverse ridge on the skull roof between the pedicles.   Brow tine typically subcylindrical, arising from the upper portion of the beam at some distance from the burr and strongly bent forwards.   Very often a more or less distinct knob below it on the anterior part of the beam, which may eventually develop into an accessory tine, close to the burr.   Some species display various degrees of reduction of the brow tine.

To this group I attribute *Megaceros verticornis* Dawkins; *M.* aff. *verticornis* from Süssenborn; *M.* aff. *verticornis* from Trimley, Red Crag; *M. dawkinsi* Newton; *M. belgrandi* Lartet from Montreuil (= *M. dawkinsi?*); *M.* aff. *belgrandi* from Taubach; *M.* aff. *belgrandi* from Laufen; *M.* aff. *belgrandi* from Tiraspol; *M. mosbachensis* Soergel; *M. solilhacus* Robert; *M. algericus* Lydekker; *M. pliotarandoides* Alessandri; *M. cazioti* Depéret; *M. cretensis* Simonelli.

The fragment from the loess of Kalouga attributed to " *Cervus* " *verticornis* by Pavlow (1906: 39) is not a *Megaceros.*

Megaceros verticornis, to be described in detail below, is the best known species. It is nearly as large as the Irish giant deer, but more primitive in the dentition. The basal portion of the antlers shows a remarkable constancy both in the form and in the position of the brow tine.   An accessory basal tine is quite exceptional. The upper portion of the antler is broadly palmated, with a faintly scalloped edge.

Megaceros aff. *verticornis* from Süssenborn (Soergel, 1927) differs from the above species by the presence of tines on the anterior edge of the palmation (the posterior portion is destroyed).   This might be perhaps a merely individual character.   The dentitions of these species are nearly identical.

Megaceros aff. *verticornis* from the Red Crag at Trimley (Dawkins, 1887) is represented by an imperfect shed antler.   This antler is very stout but does not differ otherwise from those of *M. verticornis* from the Forest Bed.   Dawkins identified it with this species, and were it not for its older age I also should not hesitate to do so.   The fossilization shows that this specimen is contemporary with the Crag, but there is no exact information on the horizon in which it was found.

Megaceros dawkinsi from the Forest Bed will also be described below.   It is smaller than *M. verticornis*; its forehead is prominent and the pedicles are strongly directed backwards.   The antlers are palmated, stout, small, and very variable in

shape. The brow tine is fluctuating. I interpret these characters as due to a secondary reduction. The dentition is hypsodont but with primitive features.

Megaceros belgrandi from Montreuil near Paris, described and figured by Belgrand (1869); *M.* aff. *belgrandi* from Taubach (Pohlig, 1892); *M.* aff. *belgrandi* from the high terrace of the Neckar near Laufen, Schwaben (Dietrich, 1909); and *M.* aff. *belgrandi* from Tiraspol (partly determined as *M. belgrandi*, partly as *M. euryceros* by Pavlow, 1906, pl. i, figs. 4, 5) are all very imperfect. They might perhaps be identical with *M. dawkinsi*. According to Dietrich the specimen from Laufen is of Upper Pleistocene age; the others come from the Middle Pleistocene.

Megaceros mosbachensis from Mosbach (Soergel, 1927) agrees with *M. verticornis* in the characters of the skull but shows some divergence in the basal portion of the antlers. The peculiar upper brow tine is present only on the right side with an accessory tine below it; on the left side there is only this accessory tine. The teeth are massive and very broad. This species was based on a single specimen.

Megaceros solilhacus from the Middle Pleistocene of Solilhac, Haute Loire (Robert, 1829) is a very large species but with relatively small antlers. The palmation is narrow, the brow tine is more or less reduced. A very fine antler has been figured by Moullade (1886) and by Freudenberg (1914) under the name *Cervus dama priscus*. The dentition is advanced, and the hyperostosis of the lower jaw is poorly developed. This species inhabited the highlands of Central France during the Riss Glaciation. I shall give soon a new description of it.

Megaceros algericus from the Middle and Upper Palaeolithic of Algeria and the Mousterian of Morocco (Arambourg, 1938) clearly shows the skull characters of this group. It reproduces also some features of *M. pachyosteus*, namely the extreme degree of hyperostosis, the small size and the shortening of the muzzle. This is well seen in a fine skull in the Palaeontological Museum in Paris, not yet described.

Megaceros pliotarandoides from the Upper Pliocene or Lower Pleistocene of Cortiglione Monferrato, N. Italy (De Alessandri, 1903) is based on an incomplete shed antler. It shows in its basal portion the characters of the group of *M. verticornis* but is very unsatisfactory and its affinities are uncertain.

Megaceros cazioti from Corsica and *M. cretensis* Simonelli are dwarf island forms. A more detailed discussion of these species will be given in another paper.

There are in addition some remains whose affinities cannot be established:
Megaceros dupuisi from the Lower (or Middle ?) Pleistocene of Rosières, France (De Grossouvre & Stehlin, 1912), is represented by some lower jaws and very imperfect fragments of antlers. The teeth are identical with those I tentatively identify with *M. savini*.

Megaceros sp. A large metatarsal from Leffe, N. Italy (Stehlin, 1930) seems the only unquestionable evidence of the occurrence of this genus in the Villafranchian of Italy.

Megaceros sp. A lower jaw from the Red Crag, in the Museum at Ipswich, not yet described. The teeth are broken off and only a part of M_1 is preserved. The length of the tooth row is as in *M. verticornis* and the horizontal ramus is very thick: its height below M_2 is 50 mm., its breadth 40 mm. The fossilization shows that this specimen was derived presumably from the lower part of the Red Crag.

Megaceros sp. from St. Prest is possibly identical with *M. dupuisi* (Stehlin, 1912: 206).

Megaceros cf. *dupuisi* from Csarnòta and Püspökfürdö (Schaub, 1932) is also very poorly represented.

A few giant deer have been described also from Switzerland (see Hescheler & Kuhn, 1948: 190–192). One of them, from the Wengimoos near Berne, is remarkable for the shortness of its neck, and is supposed to be post-glacial.

Several imperfect remains of giant deer have also been made known from Middle Pleistocene deposits of England. They all belong to more primitive species than *M. giganteus*.

According to Stehlin (1932 : 143) *Cervus martialis* Gervais (1859 : 144, pl. 21, fig. 1–8) is also a *Megaceros*. I do not feel certain of this. The lower jaw (Gervais' fig. 1) is certainly of a giant deer, but the antlers seem rather to belong to a relative of *Euctenoceros sedgwicki*.

Megaceros messinae Pohlig (1909) from Sicily seems to be another dwarf island form.

Megaceros verticornis (Dawkins)

(Figs. 23 A, B, 24–27, 28 M, N, 29 E, F, 30, 32 B, C.)

1872. *Cervus verticornis* Dawkins (pars), p. 405, fig. 2.
1882. *Cervus verticornis* Dawkins : Newton, p. 61.
1887. *Cervus verticornis* Dawkins : Dawkins (pars), pl. 5, figs. 1–3 ; pl. 6, figs. 1, 2 ; pl. 7, figs. 1, 2.
1891. *Cervus verticornis* Dawkins : Gunn (pars), pl. 2, fig. 97.
1891. *Cervus verticornis* Dawkins : Newton, p. 32.
1899. *Cervus belgrandi* Lartet : Harmer, p. 97, pl. 21.

SYNONYMY. The definition of this species has been discussed by Newton. Dawkins, in his original description, included in it also an antler on which Newton later based his *Cervus dawkinsi*. Newton chose as the type of *C. verticornis* the basal fragment of an antler from Pakefield, figured by Dawkins (1872, fig. 2).

In his later description (1887) Dawkins again included in *C. verticornis* some remains of other species. On p. 23 he recorded seven specimens with a double basal tine; exact reference was made only to a specimen in the British Museum, registered B.M. (G.D.), 33471. This register number includes a small sample of very imperfect fragments, none of which belongs to *Megaceros verticornis*. A double basal tine is quite exceptional in this species: I do not know the other specimens quoted by Dawkins, but as yet I have seen only a fragment of a young individual from Trimingham with a well-developed accessory basal tine (Fig. 26). This specimen was found after the publication of Dawkins' works.

The antler from the Red Crag at Trimley figured by Dawkins (1887, pl. 6, fig. 3) is imperfect and cannot, since it is older, be identified confidently with *M. verticornis*. The fragment from Kessingland figured by Gunn (pl. 7, fig. 2) is doubtful; it does not seem to belong to *M. verticornis*.

OCCURRENCE. This is the commonest species of *Cervidae* in the Forest Bed and has been recorded from nearly all the fossiliferous localities: Kessingland, Pakefield,

Mundesley, Overstrand, Happisburgh, Trimingham, Hopton, Sidestrand, Bacton, Cromer; it is common also in the Upper Freshwater Bed at West Runton, but is not recorded at East Runton.

The remains of this species consist for the most part of basal fragments of the antlers, either naturally shed or with fragments of the frontals. There are in addition two complete brain cases, one in the Norwich Museum (Figs. 24, 25), the second in the British Museum (Fig. 27). The latter was found in connection with the atlas, the axis and the antlers, nearly perfect, and has been described by Harmer under the name *Cervus belgrandi*, of which *Cervus verticornis* was incorrectly supposed to be a synonym.

A shed antler, in the Museum of the Geological Survey, figured by Dawkins (1887, pl. 5, fig. 2), is broken at the beginning of the palmation.

The correlation between skulls and teeth is based on the size, on their occurrence together in the Upper Freshwater Bed at West Runton, where no other species of *Megaceros* has as yet been found, and on comparison with *M.* aff. *verticornis* from Süssenborn. The dentition is represented by some lower jaws and maxillae.

Some limb bones may also possibly belong to this species.

DESCRIPTION. *Skull:* There is very little to add to Harmer's description of the skull from Pakefield. Harmer pointed out its large size and heavy form, its flat forehead and its divergent and widely spaced pedicles. The supraorbital foramina are very large and round. Two very faint ridges, starting from the coronal suture, run along the inner margins of the pedicles and vanish on the forehead. In other specimens these ridges are better developed (Fig. 25). Harmer also pointed out the lack of a transverse swelling of the frontal between the pedicles.

The other remains of skulls display little individual variations. The pedicles are generally widely spaced, but in a frontal from Pakefield (Figs. 23 A, 25 D) they are set near each other and less divergent than in the average specimens. The frontal is still flat.

Antlers: The characters of the lower portion of the antlers are remarkably constant. The brow tine arises at some distance above the burr, from the upper portion of the beam, and is strongly bent dowwards. It is rounded in cross-section and very long in a skull from Kessingland (Dawkins, 1887, pl. 7, fig. 2), the only specimen where it is complete. In many specimens there is a more or less marked knob below it, on the anterior side of the beam; this may be present on both sides or on one side only and is very variable. In a frontal from Trimingham, very much worn, it is very strong on the left side and seems to be completely lacking on the right side, but only in a young antler (Fig. 26), also from Trimingham, has it developed into an accessory lower tine. Dawkins' statement that an accessory lower tine occurs in seven other specimens has not been fully checked, but is based partly at least on incorrect identifications.

The beam is long and bears an anterior and a posterior tine, ovoidal in cross-section. The position of the anterior tine is somewhat variable (see Figs. 25 C, 27, and the figures published by Dawkins, 1887). An additional anterior tine has been recorded only in one instance (Dawkins, 1887, pl. 5, fig. 3). Above the posterior tine the beam is twisted upwards and becomes flattened, and after a short distance

FIG. 24. *Megaceros verticornis*, skull from Kessingland. Norwich Museum 364. ⅓ natural size. (See also Figs. 23 & 25.) A. Anterior aspect. B. Lateral aspect. C. Dorsal aspect.
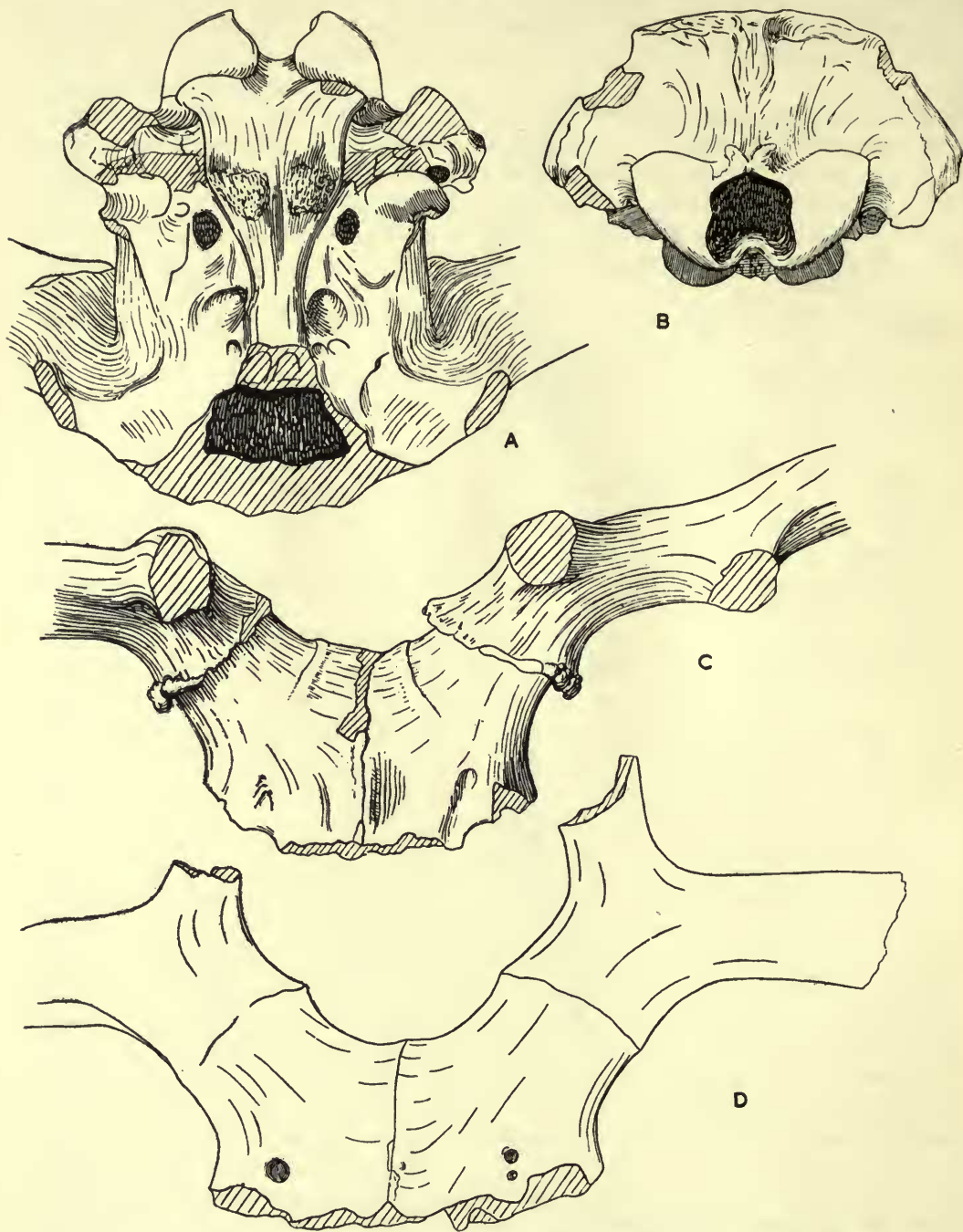
FIG. 25. *Megaceros verticornis*, skulls. A. Inferior aspect, from Kessingland.   Norwich
Museum 364. (See also figs. 23 & 24.) B. Posterior aspect, same specimen. $\frac{1}{5}$
natural size. C. Anterior aspect. West Runton, Upper Freshwater Bed. B.M.
(G.D.), M. 6099. $\frac{2}{9}$ natural size. D. Anterior aspect. Pakefield, Norwich Museum
365. $\frac{1}{8}$ natural size.

it suddenly expands into a palmation.   This palmation is preserved only in Harmer's specimen, so that we have no information on its variations.   It is very broad and thin and of a quite unusual pattern: its margin does not give origin to long tines as in most of the giant deer, but is scalloped and gently bent inwards.   The anterior edge was destroyed on both sides.   The plane of the palmation is nearly vertical
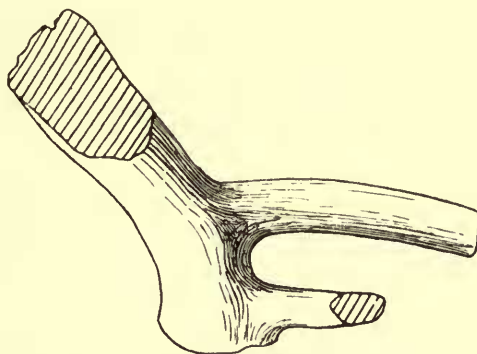

FIG. 26.   *Megaceros verticornis*, young specimen with an abnormal lower tine, Trimingham. B.M. (G.D.), Savin 713.   ⅓ natural size.
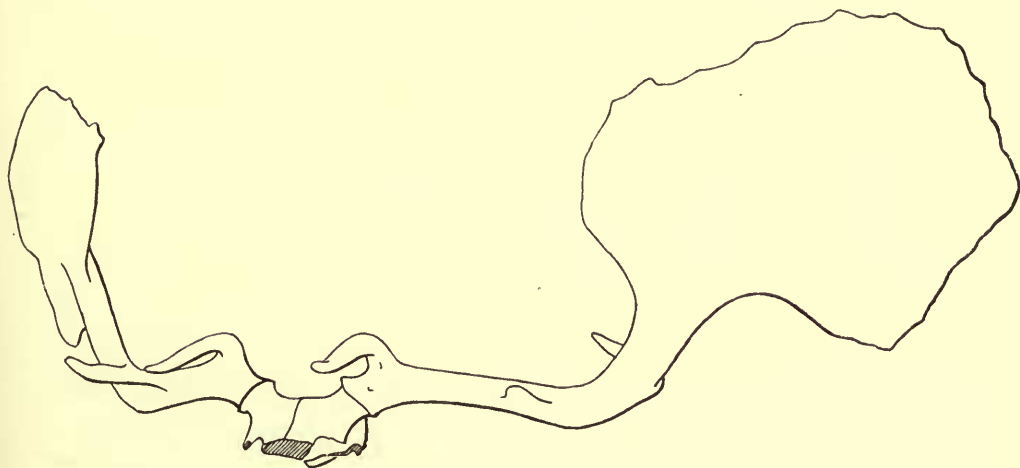
FIG. 27.   *Megaceros verticornis*, reconstruction of the specimen described by Harmer (1899), Pakefield.   B.M. (G.D.), M. 11352. $\frac{1}{14}$ natural size.

and set at 45° with the median plane of the body.   The total span in the reconstructed specimen is 228 cm.   Harmer also pointed out the rectilinear course of the blood vessels.

Harmer's specimen is rather large, but the lectotype and the skull from the Upper Freshwater Bed of West Runton (Fig. 25 c) slightly exceed it.   The antler figured by Dawkins, 1887, pl. 5, fig. 2, the most complete beyond Harmer's specimen, is on the contrary distinctly smaller.

Dentition: The remains consist of a maxilla and two lower jaws from the Upper Freshwater Bed at West Runton, a maxilla from Trimingham and some imperfect lower jaws from Pakefield, in the British Museum; a maxilla from Kessingland and probably two lower jaws, from Copton and Kessingland, in the Norwich Museum.
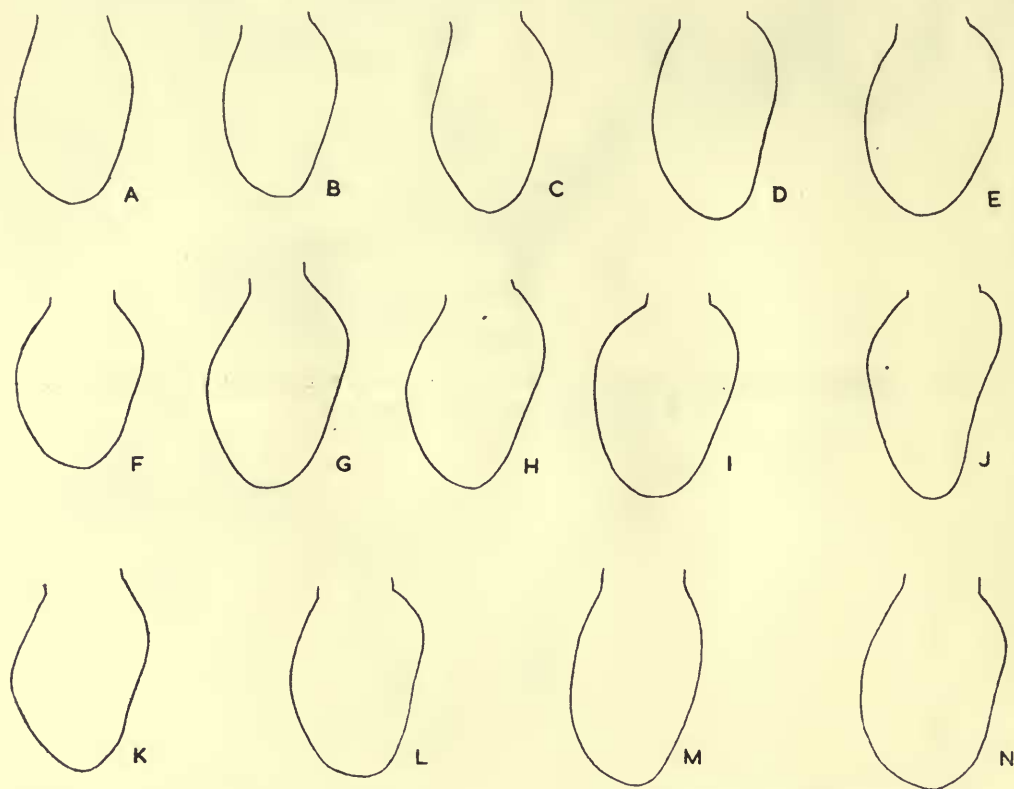

FIG. 28.   Cross-sections of lower jaws, below hinder lobe of M2.   External side to the left. $\frac{2}{3}$ natural size.   A–I. *Megaceros dawkinsi.*   A. Mundesley, B.M. (G.D.), M. 6335 (young).   B. Overstrand, B.M. (G.D.), Savin 533.   C. Sidestrand, B.M. (G.D.), M. 6224.   D. Overstrand, B.M. (G.D.), M. 6209.   E. East Runton, B.M. (G.D.), Savin 304.   F. Mundesley, B.M. (G.D.), M. 6207 (old).   G. Overstrand, B.M. (G.D.), Savin 526.   H. Mundesley, B.M. (G.D.), Savin 339.   I. Pakefield, B.M. (G.D.), M. 6501.   J. Cervid indet., Overstrand. B.M. (G.D.), Savin 421.   K & L. *Megaceros savini?*   K. Trimingham, B.M. (G.D.), M. 6220.   L. Mundesley, B.M. (G.D.), Savin 1008 (old).   M & N. *Megaceros verticornis.*   M. Overstrand, B.M. (G.D.), Savin 1198.   N. West Runton, Upper Freshwater Bed.   B.M. (G.D.), Savin 1069.

The hyperostosis of the lower jaw is moderate (Fig. 28).   The teeth are relatively small and narrow.   The basal columns are moderately developed, and in the maxilla from West Runton the upper premolars show a very faint trace of a cingulum. P_4 is somewhat intermediate between the primitive and the advanced condition.   The enamel is moderately thick, the height of the crown also moderate.
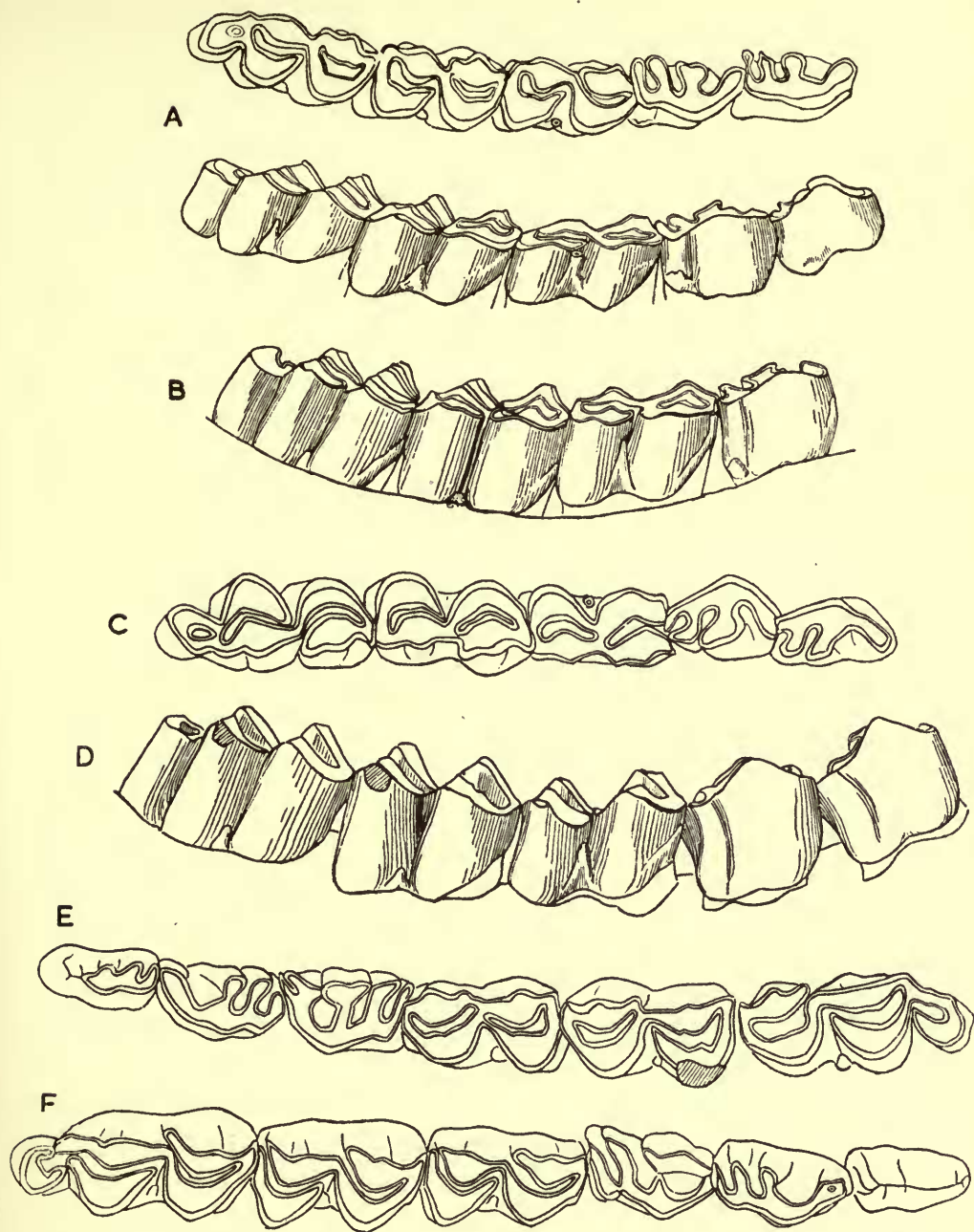
Fig. 29.   *Megaceros*, lower dentition, $\frac{10}{11}$ natural size. A. *M. dawkinsi*, Overstrand. B.M.
(G.D.), Savin 533. B. *M. dawkinsi*, Mundesley. B.M. (G.D.), M. 6231 (young).
C. *M. savini?* Trimingham, B.M. (G.D.), M. 6207. D. *M. savini?* Trimingham,
B.M. (G.D.), Savin 439. E. *M. verticornis*, West Runton, Upper Freshwater Bed.
B.M. (G.D.), Savin 1069. F. *M. verticornis*, West Runton, Upper Freshwater Bed.
B.M. (G.D.), Savin 1265.

VERTEBRAE. Atlas and axis were found in connection with Harmer's specimen. They have already been described by Harmer and are slightly smaller than the corresponding bones of *Megaceros giganteus*, but very similar in shape.

COMPARISONS. The giant deer from Süssenborn, figured by Soergel (1927, pl. 17, fig. 2 ; pl. 18, figs. 2, 4, 7), is closely related to *M. verticornis*. The skull, the dentition and the lower portion of the antlers are identical. The upper portion of the antlers in the specimen from Süssenborn is flattened and gives off two large tines from the anterior edge; the posterior portion is destroyed. In Harmer's specimen from the Forest Bed the anterior edge of the palmation is missing on both sides, but what remains of it on the right side is very thin (15–20 mm.) and is not likely to have developed large tines, which moreover would be in contrast with the general pattern of the palmation.

The systematic value of these differences is not known, as we have no idea of the range of individual variation of these forms, but no doubt they are very closely allied.

FIG. 30. *Megaceros verticornis*, lower molars, Pakefield. B.M. (G.D.), M. 6223. Natural size.

Megaceros mosbachensis, of which only a brain case with the lower portions of the antlers and some fragments of the dentition are known, also closely resembles *M. verticornis* in the characters of the skull, but differs in the antlers and teeth (see above).

The affinities between *M. verticornis* and *M. dawkinsi* are also very close and will be discussed later.

The lower jaw of *M. dupuisi* differs from that of *M. verticornis* by its smaller size and the more primitive form of P_4.

The affinities between *M. verticornis* and *M. giganteus* have been discussed by Harmer and by Soergel. It has already been shown that although these two species are related they belong to different lineages.

MEASUREMENTS OF THE TEETH :—

	B.M. (G.D.), Savin 1156 W. Runton,
Upper tooth row :	U. Freshw. Bed
Total length	124
Breadth of M²	22

Lower tooth row :	B.M. (G.D.), Savin 1069 W. Runton,	B.M. (G.D.), Savin 1265 U. Freshw. Bed
Total length . .	146 .	152
Breadth of M_2 . .	17 .	18

Megaceros dawkinsi (Newton)

(Figs. 23 C, 28 A–I, 29 A, B, 31 A, 32A, 33–36.)

1872. *Cervus verticornis* Dawkins (pars), p. 405, fig. 1.
1882. *Cervus dawkinsi* Newton, p. 54.
1882. *Cervus fitchii* Gunn MS.: Newton, p. 56.
1882. *Cervus gunni* Dawkins MS.: Newton, p. 57.
1887. *Cervus dawkinsi* Newton: Dawkins, p. 7, pl. 2, figs. 1, 2, pl. 3, fig. 3.
1891. *Alces* ? : Gunn, pl. 5, fig. 6.
1891. *Cervus fitchii* Gunn, pl. 6, fig. 1.
1891. *Cervus dawkinsi* Newton: Newton, p. 26.
1891. *Cervus fitchii* Gunn: Newton, p. 28.

SYNONYMY. This species was founded by Newton on a young antler, formerly attributed to *Cervus verticornis* by Dawkins. Other fragments determined as *Cervus fitchii* and *Cervus gunni* by Newton belong to the same species, as already pointed out by Dawkins. Newton (1891) rejected this view, but in my opinion he overestimated differences due to individual variation.

OCCURRENCE. This species is nearly as abundant and widespread as *Megaceros verticornis* and has been recorded from Bacton, Cromer, Trimingham, Sidestrand, Mundesley, Overstrand, Pakefield, Walcot and East Runton (one specimen, much rolled). A specimen in the Savin collection was found at Weybourn and was supposed to come from the Weybourn Crag; its occurrence has been discussed in the previous section. *M. dawkinsi* has not been recorded from the Upper Freshwater Bed.

The specimens consist of several portions of antlers and fragments of the frontals ; a specimen from the Walcot gap, in the museum at Norwich, bears also a part of the left parietal and temporal bones, but no complete brain cases have been found. The correlation between antlers and teeth is based on the size. The dentition is represented by several lower jaws and few fragments of the maxillae.

DESCRIPTION. The skull is distinctly smaller than that of *Megaceros verticornis*, but is represented by rather unsatisfactory specimens, so that exact measurements are possible only for the frontals. Its most striking feature is given by the convex form of the forehead and by the backward inclination of the pedicles. In the adult the pedicles are short, very massive and strongly divergent. Two shallow ridges on their inner borders, as in *M. verticornis*, are always distinct. The skull roof of the specimen reproduced on Fig. 33 A is pierced by numerous small openings; its inner surface in this region has been filled with plaster. Similar openings have been described also by Soergel (1927) in the giant deer from Mosbach and Süssenborn; they were interpreted as canals for blood-vessels.

The antlers, of which the upper portion is unknown, are stout, palmated, and very variable.   The beam is short and rounded.   Its base, unlike that of *M. verticornis*, does not grow in the same direction as the pedicle but is stretched outwards and backwards, and is thinner than the pedicle.   This is well seen also in a young specimen reproduced on Fig. 33 C.   The brow tine and the accessory lower tine are very variable, but are always more or less reduced.   The type affords the only instance of a well-developed lower accessory tine.   Very often both these tines have disappeared.   The upper tines are moderately flattened and gently twisted upwards.
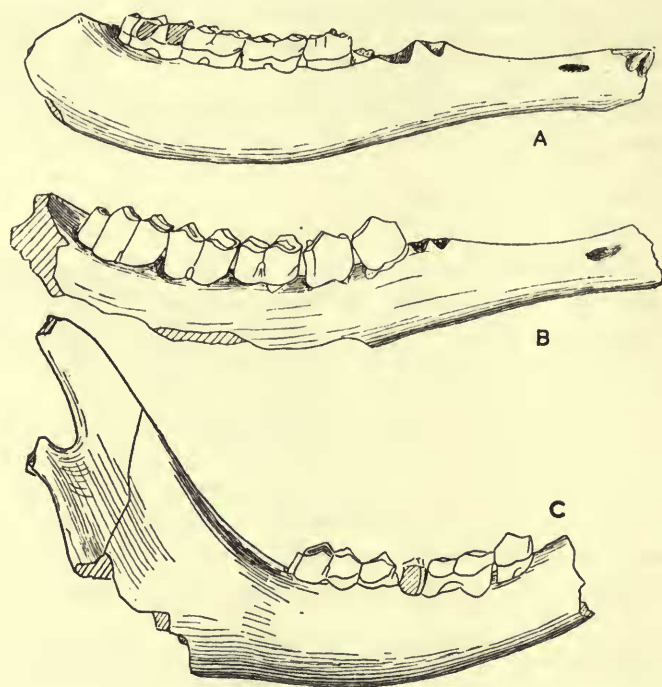

FIG. 31.   *Megaceros*, lower jaws.   ⅓ natural size.   A. *M. dawkinsi*, Overstrand.   B.M. (G.D.), Savin 526.   B. *M. savini?* Trimingham, B.M. (G.D.), Savin 439.   C. *M. savini?* Mundesley, B.M. (G.D.), Savin 1008.

There may be one or two anterior tines, and a posterior tine is not always present. The upper portion is more or less abruptly twisted upwards, sometimes resembling features of *M. verticornis*, sometimes as in Fig. 36, rather recalling *M. giganteus*. In the specimen shown on Fig. 23 C and 33 A the branching of the right antler takes place in two different planes: this is probably due to an unusual shortening of the beam between the anterior tine and the beginning of the palmation.

The teeth I refer to this species consist of several lower jaws, a fragment of a maxilla and some isolated molars.   The dental characters recall those of *M. verticornis*; the teeth are however smaller, narrower, very hypsodont, and have a thick enamel.   The lower molars bear strong basal columns and anterior folds. P_4 is

always very primitive and is characterized by the poor development of its hinder portion ; the latter is bordered by a small burr near the base of its outer wall.

The hyperostosis of the lower jaw is well marked (Fig. 28).

AFFINITIES.   Dawkins (1887) pointed out the general resemblance of the antlers with those of *M. giganteus*, but concluded that the affinities between these two species are not very close.

As he limited his observations to the antlers, he failed to perceive the affinities between *M. dawkinsi* and *M. verticornis*, which moreover was imperfectly known until the discovery of Harmer's specimen, ten years later.
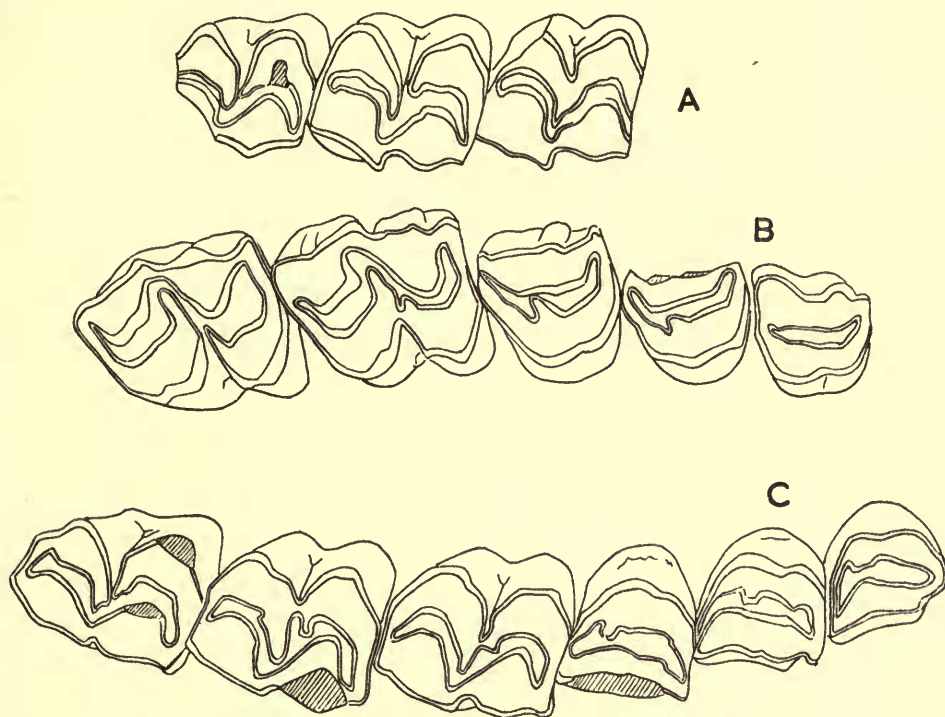

FIG. 32.   *Megaceros*, upper dentition.   Natural size.   A. *M. dawkinsi*, Trimingham, B.M. (G.D.), Savin 7.   B. *M. verticornis ?*   Trimingham, B.M. (G.D.), Savin 942. c. *M. verticornis,* West Runton, Upper Freshwater Bed.   B.M. (G.D.), Savin 1156.

The characters of the skull leave little doubt that *Megaceros dawkinsi* belongs to the group of *M. verticornis*.   The antlers support this conclusion : it has been shown that a small brow tine, similar to that of *M. verticornis*, is not uncommon.   This never occurs in the group of *M. giganteus*.

However, *Megaceros dawkinsi*, in spite of its small size, is not primitive, and does not belong to the same lineage as *M. verticornis*.   The dentition displays simultaneously primitive and advanced features; the lower pre-molars are perhaps of the most primitive pattern yet known, but both the hypsodonty and the thickness of the enamel are no doubt advanced features.   There is no hint of the broadening

FIG. 33. *Megaceros dawkinsi*, parts of the skull. ⅓ natural size. A. Dorsal and anterior views. Sidestrand, B.M. (G.D.), M. 6302. (See also Fig. 23.) B. Anterior view. Mundesley, B.M. (G.D.), M. 6424. C. Anterior view. Mundesley, B.M. (G.D.), Savin 1883 (very young). D. Dorsal view. Trimingham, B.M. (G.D.), Savin 2207 (very old). E. Anterior view, same specimen.
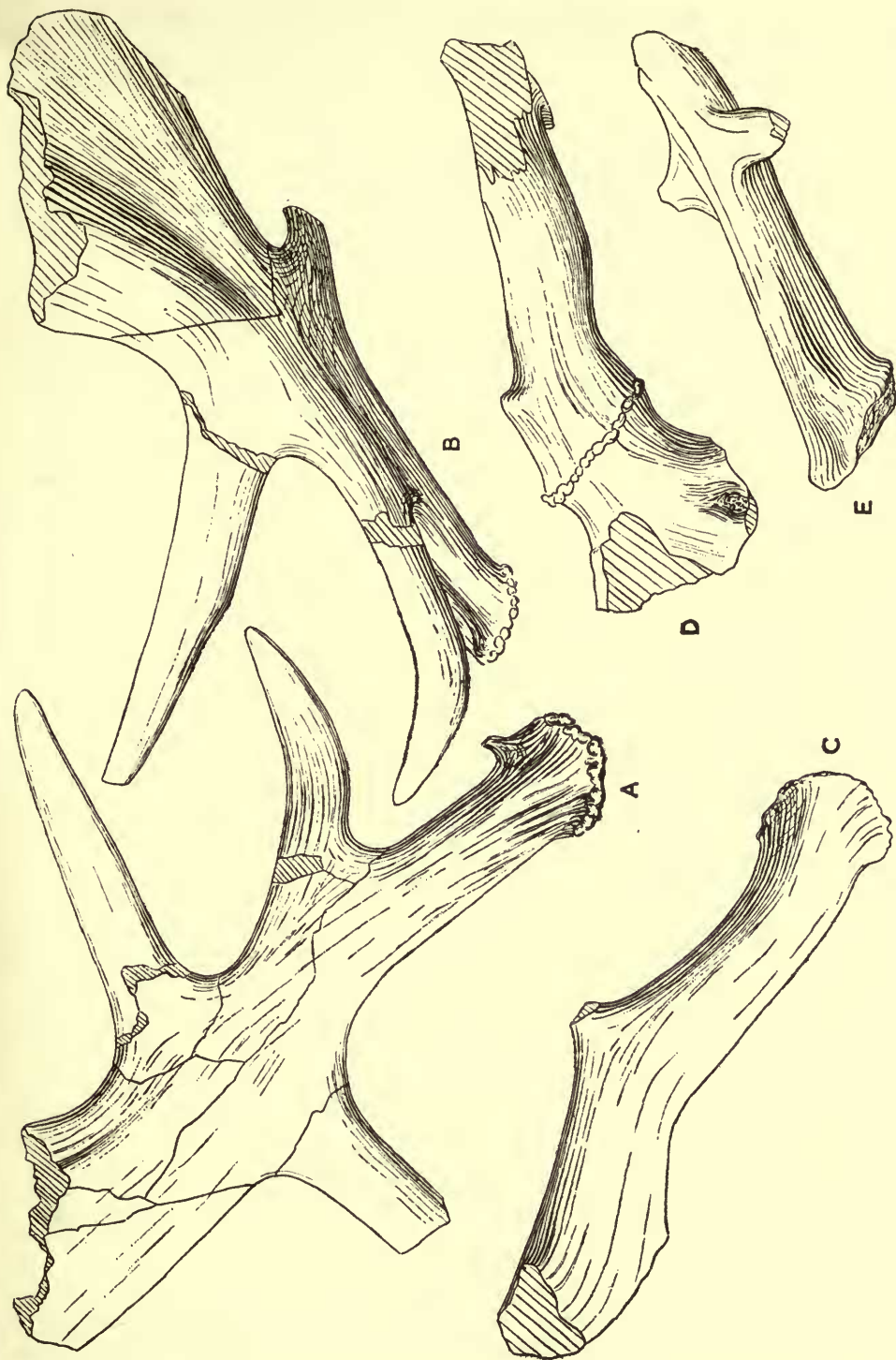
FIG. 34. *Megaceros dawkinsi*, antlers. ¼ natural size. A. Mundesley, B.M. (G.D.), Savin 1720. Anterior view. B. The same specimen, oblique, posterior view. C. Mundesley, B.M. (G.D.), Savin 1291. D. Mundesley, B.M. (G.D.), Savin 2186. E. Bacton, B.M. (G.D.), Savin 1897.

of the molars, undergone by *Megaceros giganteus* and *M. mosbachensis*.   Nor can the antlers be considered primitive.   The pedicles are disproportionately strong for their size; moreover, in cross-section the beam is thinner than the pedicle and is

FIG. 35.   *Megaceros dawkinsi*, left antler, seen obliquely from the outer side.   Trimingham, B.M. (G.D.), Savin 1820.   ⅓ natural size.

FIG. 36.   *Megaceros dawkinsi*, reconstructions of the antlers based on the specimens of Figs. 33 & 34.   ⅛ natural size.

stretched backwards—two common features in the deer with reduced antlers.   The unusually high instability of the tines is also a character peculiar to regressed antlers.

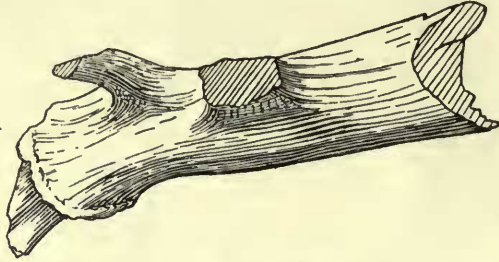Whether this regression of *M. dawkinsi* was due to inner factors or to influence of the environment can hardly be stated.   The characters of the dentition suggest habits of life in open, grassy lands, rather than in woodlands; this is a rather unusual habitat for deer.

Megaceros belgrandi and several related forms from Central and Eastern Europe, listed above, are closely similar to *M. dawkinsi* and possibly identical with it, but their remains are very imperfect.

A striking similarity with the antlers of *M. dawkinsi* is shown by an antler of *Cervus cazioti* from the cave of Nonza in Corsica, figured by Depéret (1897*a*), which, however, is less than half the size of the antlers of *M. dawkinsi*.   *Cervus cazioti* is no doubt a dwarf island form.   Also its dentition recalls *M. dawkinsi*.

MEASUREMENTS:—

	B.M. (G.D.) M. 6302 Sidestrand
Frontal	
Minimal breadth beneath the pedicles .	164

Lower jaws	B.M. (G.D.), Savin 526 Overstrand	B.M. (G.D.), M. 6224 Sidestrand	B.M. (G.D.), Savin 339 Mundesley	B.M. (G.D.), Savin 533 Overstrand
Total length of the tooth row .	128	134	125	123
Breadth of M_2	15	15	15	14, 5

Megaceros savini (Dawkins)

(Figs. 23 D, 28 K, L, 29 C, D, 37–40.)

1887. *Cervus savini* Dawkins (pars), p. 11, pl. 3, fig. 3, 5 ?
1891. *Cervus savini* Dawkins : Gunn (pars), pl. 7, figs. 4, 5.
1891. *Cervus* sp. Gunn, pl. 4, fig. 101, pl. 6, fig. 2.
1891. *Cervus savini* Dawkins : Newton, p. 30.

SYNONYMY.   Dawkins included in this species also an antler of *Euctenoceros ctenoides* (1887, pl. 3, fig. 4) and a fragment of a young specimen whose identity is uncertain (pl. 3, fig. 2), but Newton pointed out that these identifications are incorrect.   Gunn attributed to it a frontal (pl. 4, fig. 102), which might possibly belong to a red deer.

OCCURRENCE.   This species is fairly frequent and is represented by not less than twenty antlers in the British Museum and at Norwich.   Eleven of them were found at Trimingham, the others at Sidestrand, Overstrand, Mundesley and Kessingland. A frontal from Kessingland (Figs. 23 D, 37) and possibly another frontal from Pake- field (Dawkins, 1887, pl. 3, fig. 5) represent all that is known of its skull.

The remains of dentition I tentatively refer to this species consist of three lower jaws from Trimingham and Mundesley, in the British Museum.

DESCRIPTION.   The frontal, which indicates an animal of about the same size as *Megaceros verticornis*, clearly shows the hollowed forehead of the group of *Megaceros giganteus*.   The identification of the frontal (Figs. 23 D, 37) is made possible by the basal portion of the antler.

The antlers include specimens of all ages.   The type (Dawkins, 1887, pl. 3, fig. 3) is of medium size, but the largest specimens, represented by basal fragments (Fig. 38 A, and a more imperfect fragment in the Norwich Museum, from an unknown
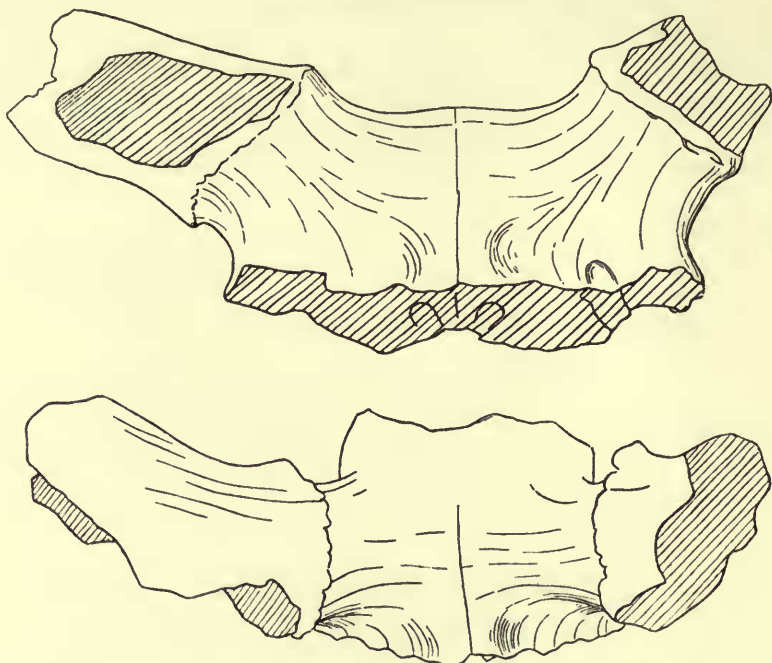
FIG. 37.   *Megaceros savini*, frontal, Kessingland.   Norwich Museum 321.
(See also Fig. 23.)   ⅓ natural size.

locality), attained the size of *Megaceros verticornis* and *M. giganteus*.   The beam is flattened and hollowed below and bears a prominent ridge on its anterior side. The brow tine (Fig. 38 C, D, and Gunn, 1891, pl. 6, fig. 2) branches off close to the burr; it is flattened, broadly expanded into a small palmation, and set horizontally.   It is very often broken off at the base, and I do not know any specimen where it is complete.   The section of its base is triangular, with the longer side above.   The antlers are widely divergent, as in *M. giganteus* and in *M. verticornis* (Fig. 39).   The anterior and posterior tines are much flattened; above the posterior tine the beam is bent upwards, becomes still more flattened and branches into two terminal tines, apparently of equal size.

The teeth I tentatively refer to this species are intermediate in size between those of *M. verticornis* and those of *M. dawkinsi*.   The distinction is not sharp, and in

their extreme variations these species, especially *M. verticornis* and *M. savini*, may perhaps overlap. The lower tooth row is identical with that of *Megaceros dupuisi* (Stehlin, 1912). P_4 is primitive. The teeth I have seen are rather worn, but they do not seem to be hypsodont. The enamel is of medium thickness.
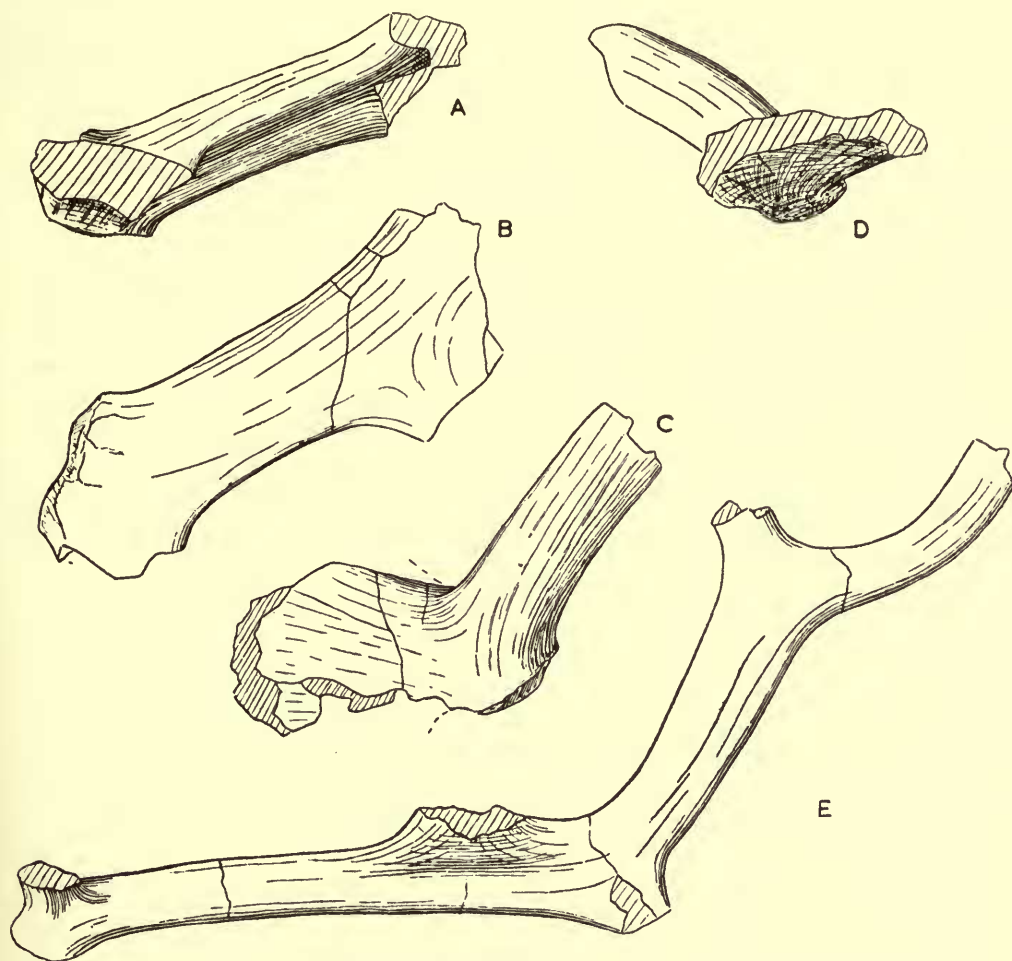
FIG. 38. *Megaceros savini*, antlers. $\frac{1}{4}$ natural size. A & B. Trimingham, large specimen. B.M. (G.D.), Savin 1422. C & D. Overstrand, medium sized specimen. B.M. (G.D.), Savin 1880. E. Trimingham, young specimen. B.M. (G.D.), Savin 1241.

Two imperfect maxillae from Trimingham might perhaps belong to this species.

MEASUREMENTS:—

	B.M. (G.D.), M. 6220 Trimingham
Lower jaw :	
Total length . . .	135
Breadth of M_2 . .	16

FIG. 39.   *Megaceros savini*, reconstruction of the holotype, B.M. (G.D.), M. 6093, and of the specimens of Fig. 38. $\frac{1}{10}$ natural size.
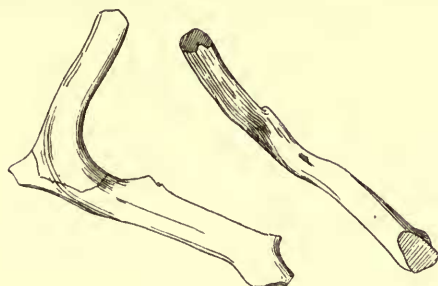
FIG. 40.   *Megaceros savini ?*   Very young specimen.   Bacton, B.M. (G.D.), Savin 910.
$\frac{1}{5}$ natural size.

FIG. 41.   *Megaceros*, limb bones. $\frac{1}{3}$ natural size.   A. *M. verticornis* or *savini*.   Right radius.   No locality, B.M. (G.D.), Savin 1462.   B. *M. verticornis* or *savini*.   Right metacarpal, Trimingham.   B.M. (G.D.), Savin 1104.   C. *M. dawkinsi ?*   Right metacarpal, Mundesley.   B.M. (G.D.), Savin 2024.   D. *M. verticornis* or *savini*, Left metapodial, Trimingham.   B.M. (G.D.), Savin 1450.

Megaceros incertae sedis

(Fig. 41 A–D.)

LIMB BONES.   Fourteen complete limb bones may be attributed to the genus *Megaceros* for their large size and heavy form.   They are: two radii, three meta-carpals and four metatarsals in the British Museum; a metacarpal and a tibia in the Norwich Museum; a radius, a metacarpal and a metatarsal in the Museum of the Geological Survey.   The metapodials are characterized by the broad form of their distal articulations and are easily recognizable.

The larger bones are of the same size as *Megaceros giganteus* and may be attributed to *M. verticornis* or to *M. savini*; the smaller ones probably belong to *M. dawkinsi*, or to females of the larger species.

MEASUREMENTS:—

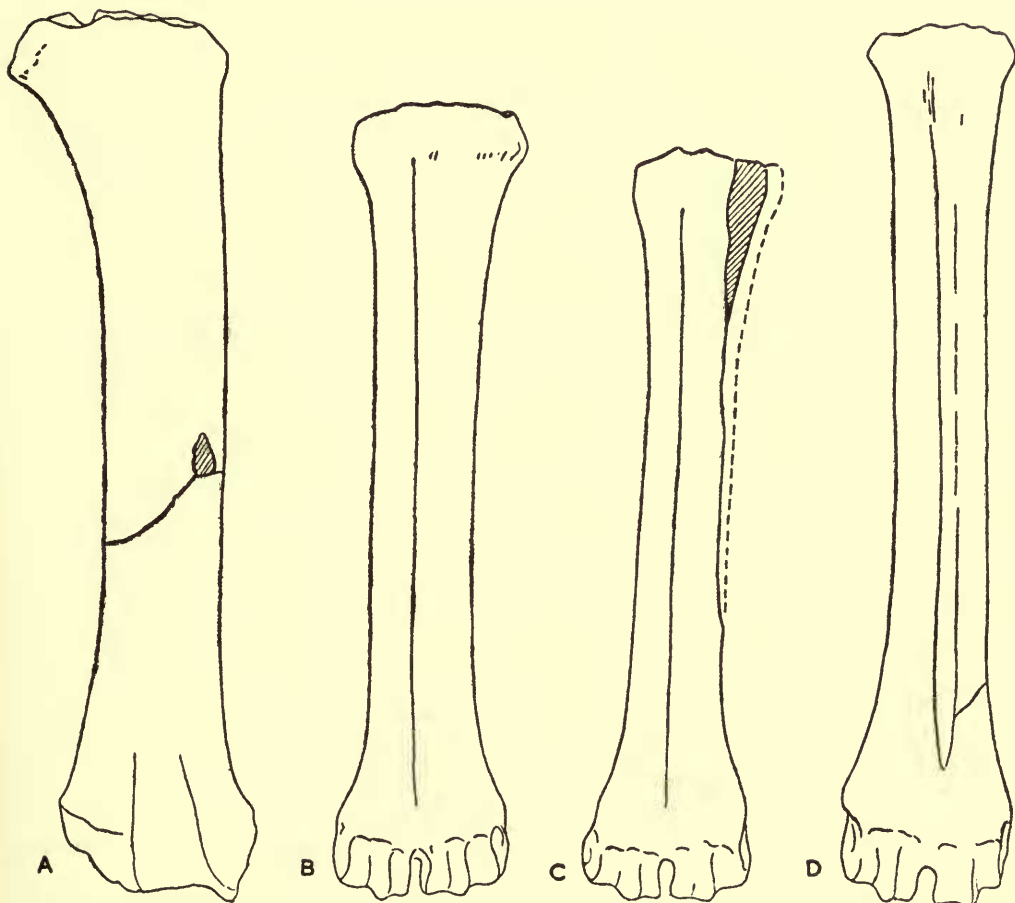| Radius :	B.M. (G.D.), Savin 464. Trimingham		B.M. (G.D.), Savin 1462. (No locality)		G.S. 21688. Kessingland
Total length . . .	340	.	349	.	320
Proximal breadth . .	79	.	82	.	—
Distal breadth . . .	—	.	73	.	—

Metacarpal :	B.M. (G.D.), Savin 1104. Trimingham		B.M. (G.D.), Savin 376. Sidestrand		B.M. (G.D.), Savin 2024. Mundesley
Total length . . .	304	.	293	.	286
Proximal breadth . .	64	.	56	.	—
Distal breadth . . .	68	.	60	.	63

	G.S. TF/55. Mundesley		Norwich Museum 531. (No locality)		B.M. (G.D.), Savin 1885. Sidestrand
Total length . . .	271	.	310	.	261
Proximal breadth . .	51	.	70	.	48
Distal breadth . . .	58	.	74	.	52

Tibia :	Norwich Museum 526. (No locality)
Total length . . .	482
Distal breadth . .	81

Metatarsal :	G.S. 21684. Kessingland		B.M. (G.D.), M. 6491. Trimingham		B.M. (G.D.), Savin 1450. Trimingham
Total length . . .	348	.	358	.	345
Proximal breadth . .	57	.	59	.	55
Distal breadth . . .	65	.	67	.	64

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Cervidae *incertae sedis*

" *Cervus* " *obscurus* n. sp.

(Figs. 42–45.)
</div>

Syntypes. B.M. (G.D.), Savin 195, Mundesley (Fig. 42 A, B); B.M. (G.D.), M. 2321, Forest
    Bed : no exact locality (Fig. 42 C–E) ; B.M. (G.D.), M. 6421, Overstrand (Fig. 43).

Additional specimens. Two lower portions of shed antlers and three basal
fragments of antlers with the frontals; two of these (Fig. 44 C, D) possibly belong
to the same individual.

Occurrence.   Bacton, Mundesley, Sidestrand and Overstrand.   In addition, an
antler of doubtful attribution from Trimingham.

Diagnosis.   A cervid of large size characterized by a small lower basal tine
directed downwards, a large upper basal tine strongly twisted outwards, a massive
beam and an upper tine set far apart from the basal tines.

Description.   This is a species of very unusual features.   The size is large and
the forms are massive as in *Euctenoceros dicranios* and *ctenoides*.   The forehead is
marked by a prominent median suture and two shallow ridges along the inner
borders of the pedicles, as in *Megaceros verticornis* and its relatives, but is narrower.
A small tine is given off close to the burr, at a wide angle with the beam, and is
inclined inwards and downwards.   A second basal tine, much more robust, arises
at some distance from the burr and is strongly bent outwards.   It is rather long
and is flattened at its end.   The beam is massive, straight, and ovoidal in cross-
section, with the major axis set vertically.   A third tine, directed upwards, is given
off at a very great distance from the burr.   The grooves of the blood-vessels are
shallow.

The remaining parts of the frontals enable one to reconstruct the position of the
antlers.   The beams diverge at about 45° from the median plane of the body.

The antler from Trimingham which I doubtfully identify with this species (Fig.
44 A, B) differs in the characters of the lower tines.   The lower tine arises at some
distance from the burr; a second tine arises from the inner side, near its base.
This tine corresponds for its position to the small knob between the two basal tines
of the syntype of Fig. 42 C, D, E.

Affinities.   The systematic position of this species is quite uncertain.   No
doubt it does not belong to the genus *Cervus* in the restricted sense defined in the
previous pages.   The lower portion of the antlers recalls that of *Megaceros verti-
cornis*, but the characters of the upper portion of the antlers and of the forehead
rule out any relationship with *Megaceros*; they rather point to some affinity with
Euctenoceros, but this question is still open.

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Specimens of Doubtful Attribution
</div>

Lower jaws.   Two lower jaws from Overstrand and Trimingham (Figs. 28 J,
46, 47) might belong either to " *Cervus* " *obscurus* or to *Euctenoceros sedgwicki*.   They
both belong to young but fully grown specimens.   The teeth are massive and
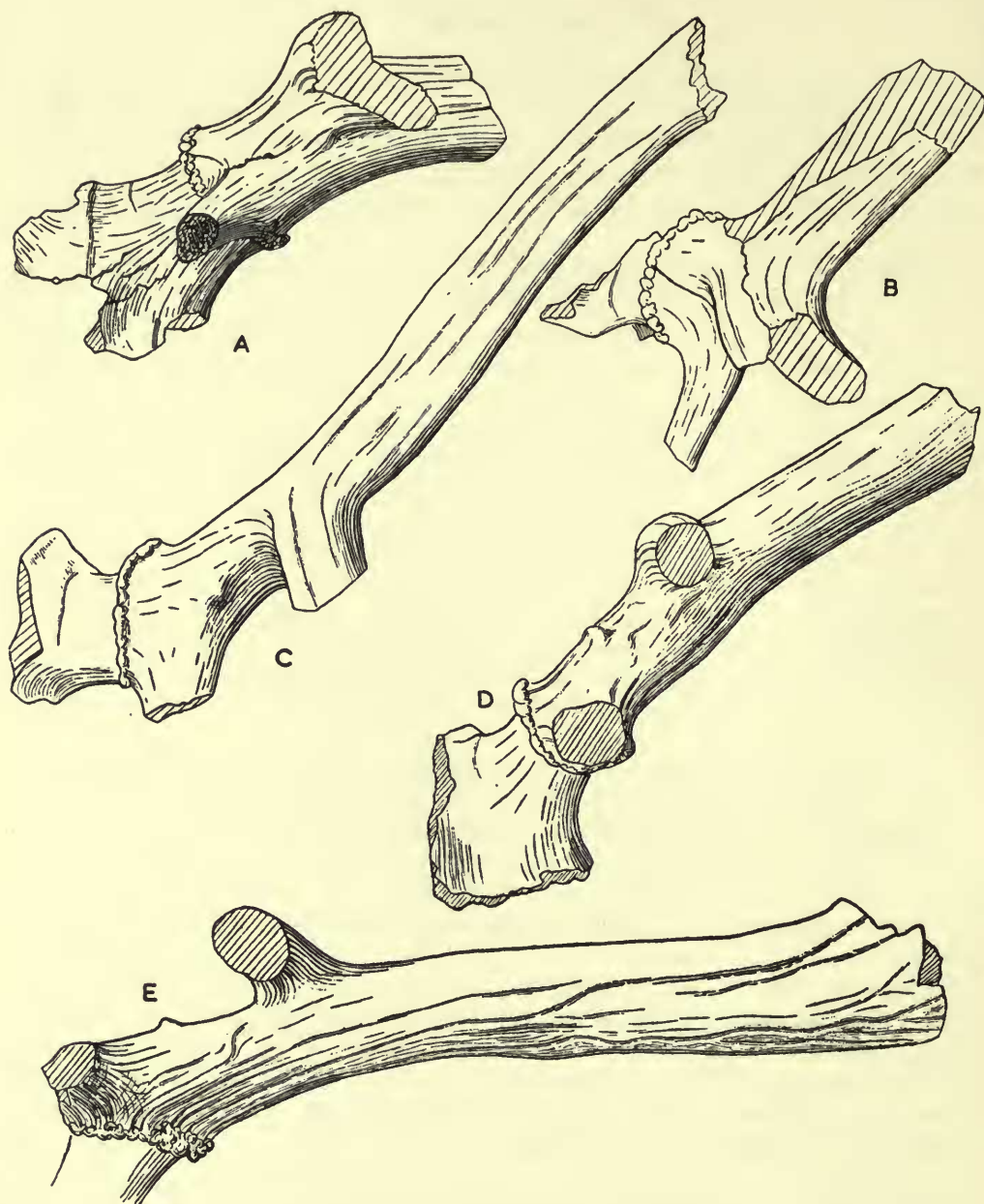
FIG. 42.   " *Cervus* " *obscurus*, two of the syntypes.   ¼ natural size.   A & B. Mundesley, B.M. (G.D.), Savin 195.   C, D & E. Forest Bed, B.M. (G.D.), M. 2321.
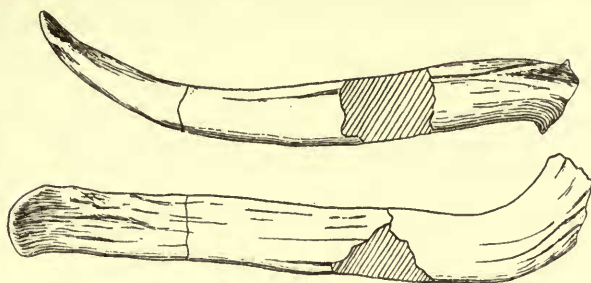
FIG. 43.   " *Cervus* " *obscurus*.   Syntype, Overstrand.   B.M. (G.D.), M. 6421.
¼ natural size.
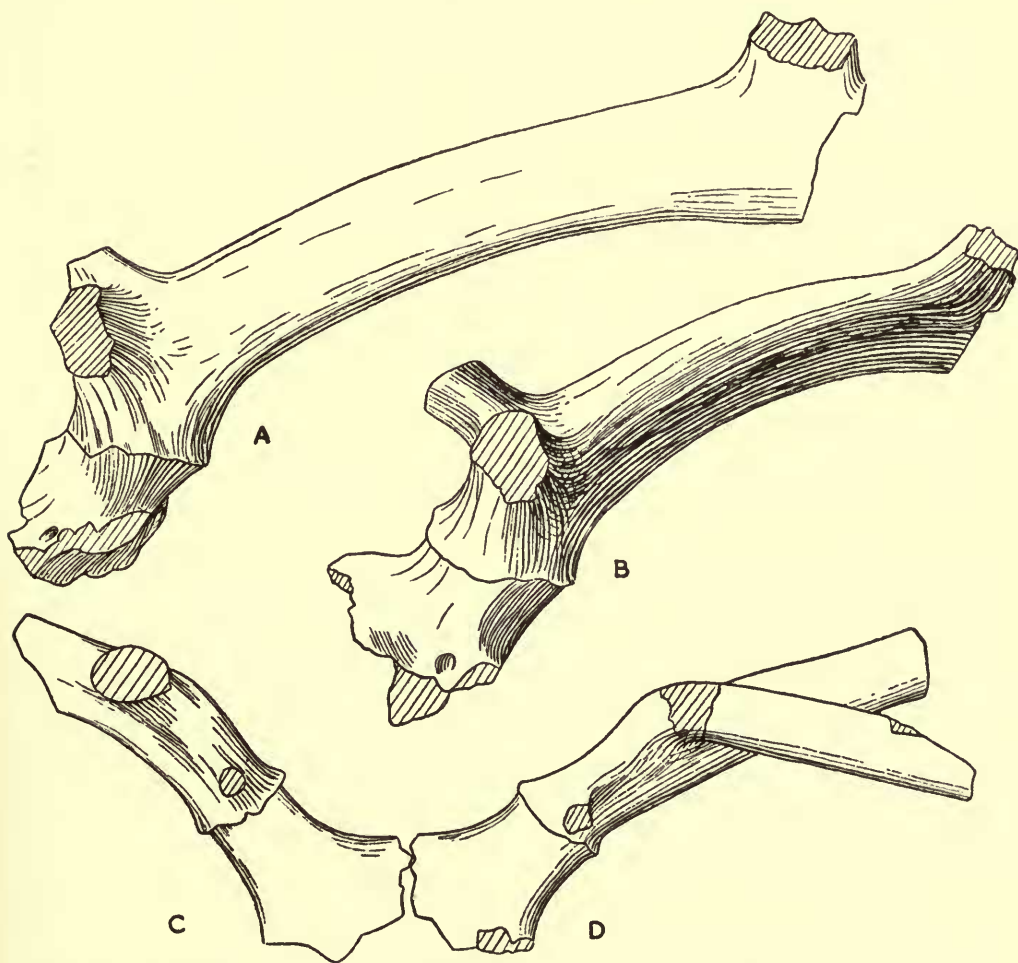
FIG. 44.   A & B. " *Cervus* " cf. *obscurus*, Trimingham.   B.M. (G.D.), M. 6400.   C.
" *Cervus* " *obscurus*, right antler of young specimen, Mundesley.   B.M. (G.D.),
M. 6307.   D. " *Cervus* " *obscurus*, left antler of a young specimen, Mundesley.   B.M.
(G.D.), M. 6315, probably both belonging to the same individual.   ¼ natural size.

seem to be slightly more hypsodont than those from East Runton which I tentatively refer to *Euctenoceros ctenoides*. P_4 has a complete internal wall and the molars bear a strong anterior ridge.   The ramus is depressed and thick, and its cross-section closely resembles that of the lower jaws of *Euctenoceros* from the Upper Valdarno (Azzaroli, 1948, fig. 11, no. 3).   The jaw from Trimingham, which is more complete, is distinguished by a large coronoidal process.   The breadth of M_2 is 17 mm.
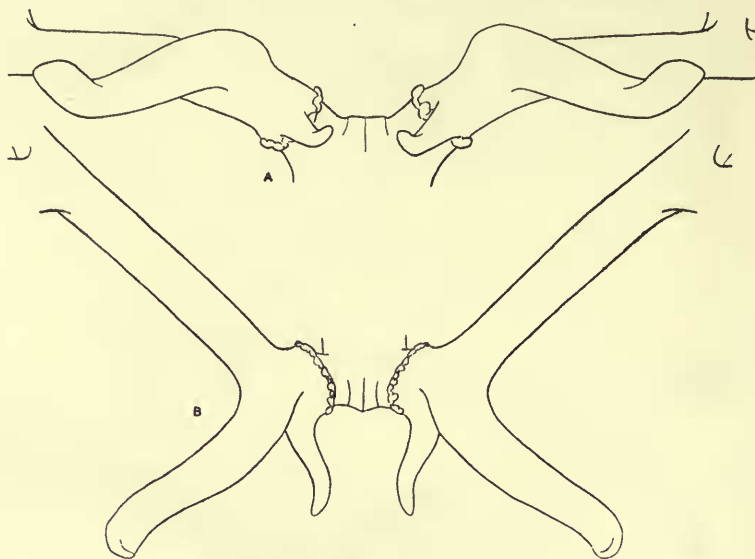
FIG. 45.   " *Cervus* " *obscurus*, tentative reconstruction, based on the syntypes.   ⅛ natural size.   A. Anterior view.   B. Dorsal view.

BRAIN CASE.   The identification of a brain case from Trimingham (B.M. (G.D.), M. 6303) is uncertain.   The shortness of the pedicles gives evidence that it belonged to a fully grown specimen; they are, however, too small for *Euctenoceros ctenoides*, *E. sedgwicki* or " *Cervus* " *obscurus*.   Moreover, the forehead is hollowed, and bears no trace of the ridges which distinguish the latter species.   *Euctenoceros tetraceros* is not recorded at Trimingham, and the supraoccipital crest of the specimen in question is much stronger than that of the skull roof from East Runton I tentatively identify with *E. tetraceros*.   The brain case from Trimingham might possibly belong to *Cervus* cf. *elaphus*; however, it exceeds the size even of the largest specimens from Val di Chiana (Azzaroli, 1948).

MEASUREMENTS:—

Occipital breadth	156
Occipital height	93
Minimal frontal breadth	152
Breadth of the brain case between the parietals .	104
Breadth of the condyles	89

Fig. 46.   Cervid indet., lower dentition.   Trimingham, Norwich Museum 45.   Natural size.
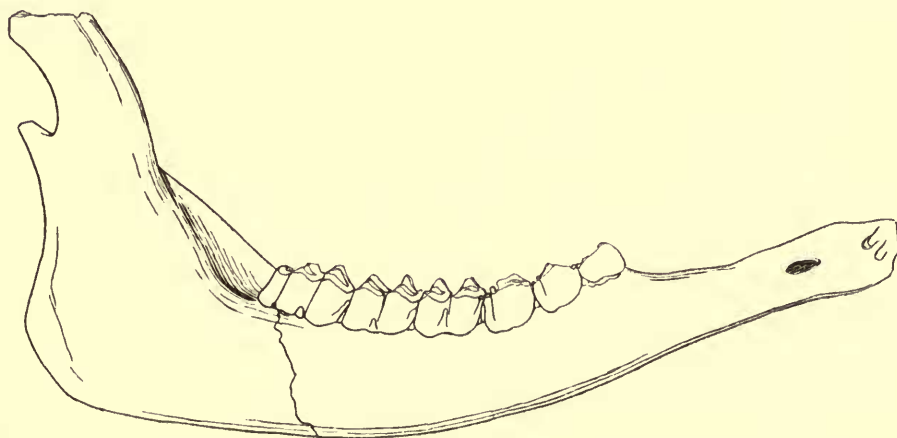
Fig. 47.   Cervid indet., Trimingham, Norwich Museum 45.   (See also
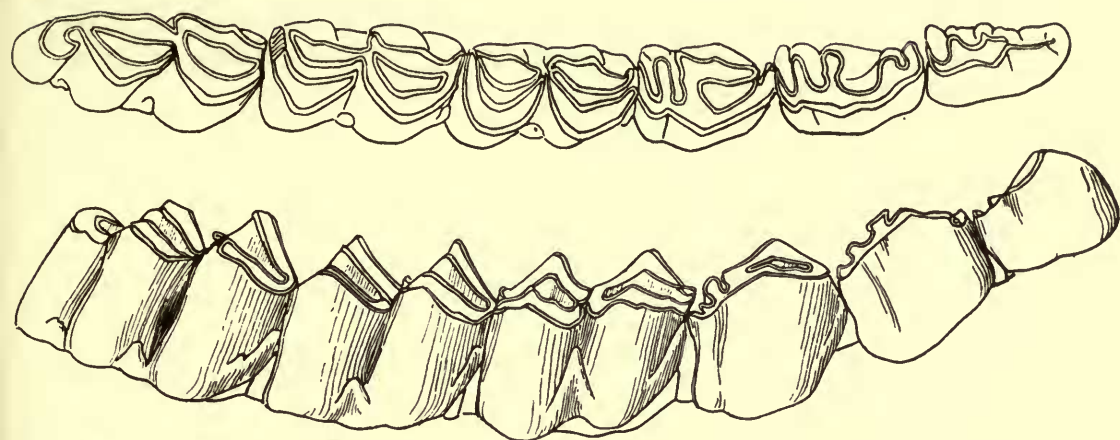Fig. 46.)   ⅛ natural size.

LIMB BONES.   An account of the complete limb bones is given in the following table of measurements; some of them have been reproduced in Fig. 48.   The metapodials are easily recognizable from those of *Megaceros* by the narrower form of their distal articulation, but a more precise determination is difficult and can be based only on the proportions.   They might be attributed to *Euctenoceros*, to the red deer, or to " *Cervus* " *obscurus*.
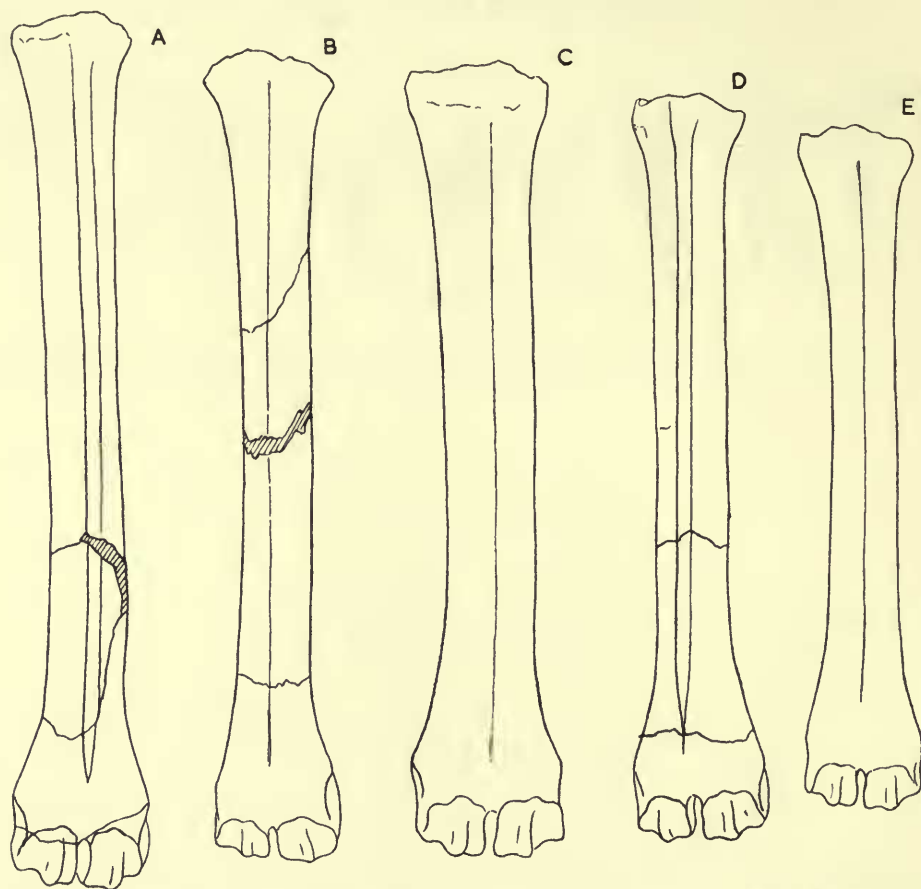
FIG. 48.   Cervids indet., limb bones.   ⅓ natural size.   A. Left metatarsal, West Runton, Upper Freshwater Bed.   B.M. (G.D.), Savin 1643.   B. Left metacarpal, Trimingham. B.M. (G.D.), Savin 2168.   C. Left metacarpal, Trimingham.   B.M. (G.D.), M. 6473. D. Right metatarsal, Overstrand.   B.M. (G.D.), Savin 773.   E. Right metacarpal, East Runton.   B.M. (G.D.), M. 6476.

Some bones from Trimingham and from West Runton (B.M. (G.D.), Savin 2168, 1424, 1643) are long and slender like those of *Libralces gallicus*, but their shape is quite different and leaves little doubt that they belong to a cervine.   Their identi-fication is puzzling; *Euctenoceros ctenoides* and *E. tetraceros* can be excluded, and an identity with the red deer seems extremely improbable, although only this

among the five species quoted above has been found in the Upper Freshwater Bed at West Runton. *Euctenoceros sedgwicki* was presumably as heavy an animal as the largest representatives of its genus. An identification with " *Cervus* " *obscurus* seems less improbable.

MEASUREMENTS:—

Radius :	B.M. (G.D.), 1105. Trimingham	B.M. (G.D.), M. 6469. Sidestrand
Total length	337	325
Proximal breadth	70	—
Distal breadth	63	61

Metacarpal :	B.M. (G.D.), Savin 2168. Trimingham	B.M. (G.D.), Savin 1424. Trimingham	B.M. (G.D.), M. 6476. East Runton		B.M. (G.D.), M. 6473. Trimingham	
Total length	321	316	267	283	306	291
Proximal breadth	51	53	45	50	55	52
Distal breadth	50	53	45	50	57	53

Femur :	B.M. (G.D.), Savin 1446. Trimingham
Total length	360
Proximal breadth	103
Antero-posterior diameter of the distal epiphysis	85

Metatarsal :	B.M. (G.D.), Savin 1685. Trimingham	B.M. (G.D.), Savin 1071. Overstrand	B.M. (G.D.), Savin 773. Overstrand	B.M. (G.D.), M. 6490. Sidestrand
Total length	310	307	311	265
Proximal breadth	42	41	45	39
Distal breadth	—	47	52	—

	B.M. (G.D.), M. 6495. East Runton		B.M. (G.D.), Savin 1643. West Runton, U. Freshw. Bed
Total length	293	293	347
Proximal breadth	44	41	46
Distal breadth	50	47	54

Cervid cf. *Dama nestii nestii*

(Fig. 49.)

1882. *Cervus etueriarum* ? Croizet & Jobert : Newton, p. 55.
? 1889. *Cervus rectus* Newton, p. 145, fig. 1, 1a.
? 1891. *Cervus rectus* Newton : Newton, p. 30, pl. 4, fig. 1.
SYNONYMY. Newton's *Cervus rectus* is based on a very young specimen, probably of this species, as may be seen by comparison of the type with fig. 1 n° 1, 2 in Azzaroli, 1948.

OCCURRENCE. Seven lower portions of antlers and a fragment of the upper portion, from East Runton; two basal fragments from Sidestrand and one from
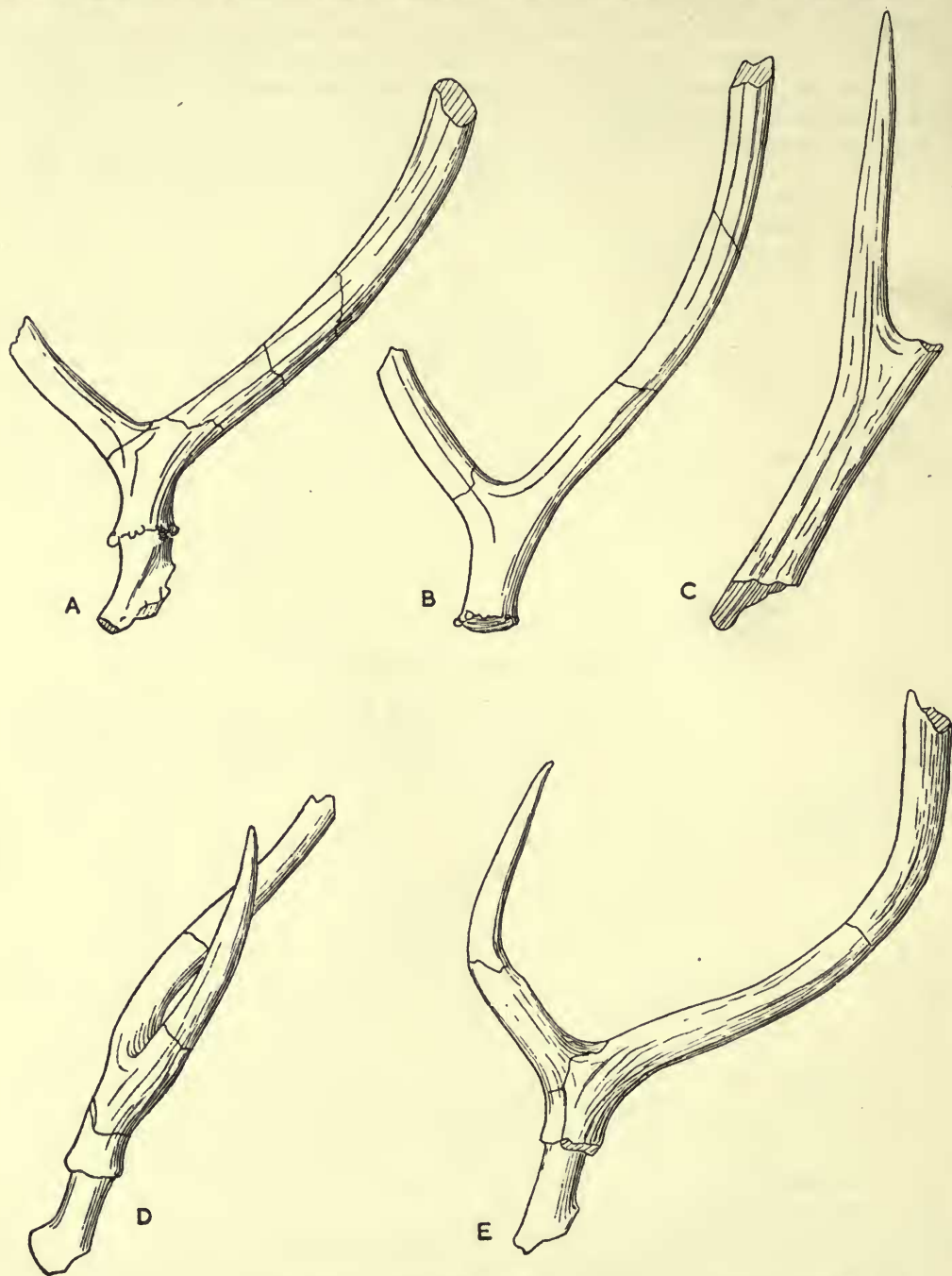
FIG. 49. Cervid cf. *Dama nestii nestii*, antlers. ¼ natural size. A. Left antler, Mundesley. B.M. (G.D.), Savin 1164. B. Left antler, East Runton. B.M. (G.D.), M. 6365. C. Fragment of the upper portion of a left antler, East Runton. B.M. (G.D.), M. 6389. D & E. Left antler, East Runton. B.M. (G.D.), M. 6568.

Mundesley. Probably two isolated M_3 and some imperfect metapodials from East Runton.

DESCRIPTION AND COMPARISONS. This species is poorly represented. The antlers correspond with those of *Dama nestii nestii* from the Upper Valdarno and Olivola (Azzaroli, 1948) for the position and development of the brow tine and the regular helicoidal torsion of the beam. Also the fragment of the upper portion agrees with the terminal fork of this subspecies; the curvature of the beam and the characters of the fork give evidence that the bifurcation took place in a transverse plane. If so, the antler had four tines.

The other species, with which this species can be compared are: *Cervus philisi* from Sénèze (Schaub, 1942), *Cervus rhenanus* from Tegelen (Hooijer, 1947) and *Cervus perolensis* from the Auvergne (Bout & Azzaroli, 1953). *Cervus philisi* differs in the stronger development of the brow tine, the straighter form of the beam, and the characters of the upper portion of the antlers. *Cervus rhenanus*, whose antlers are more imperfectly known, differs mainly in the higher position of the brow tine, and *Cervus perolensis*, also imperfectly known, in the stronger development of the brow tine. These three species are rather primitive and their relationships are not yet clear.

Cervid cf. *Dama clactoniana* Falc.

(Fig. 50)

I include here several specimens of the size of a fallow deer. Their identification is somewhat uncertain and they might possibly include more than one species. Their age is also uncertain, but at least the specimens from the Upper Freshwater Bed are certainly post-Villafranchian.

ANTLERS (Fig. 50). Three basal fragments from Bacton, Trimingham, and West Runton (Upper Freshwater Bed). They are distinguished by a very stout basal bifurcation and a strong curvature of the brow tine. The pedicles are small. The antlers from Bacton and from West Runton are disproportionately large for their pedicles and probably belong to old individuals.

TEETH. Several isolated teeth and a complete lower tooth row from the Upper Freshwater Bed at West Runton; two imperfect lower jaws, from Overstrand and Trimingham. The lower molars bear well-developed basal columns. The P_4 from Overstrand is primitive, two P_4 from West Runton are advanced. The total length of the lower tooth row from West Runton is 100 mm.

LIMB BONES. Two perfect metacarpals, from Overstrand and Trimingham. Fragments of about the same size occur in the Upper Freshwater Bed of West Runton.

MEASUREMENTS:—

	B.M. (G.D.), M. 6475. Overstrand	B.M. (G.D.), Savin 1399. Trimingham
Metacarpal		
Total length	232	235
Proximal breadth	35	35
Distal breadth	35	35

COMPARISONS.   In the Villafranchian fauna only *Dama nestii eurygonos* (Azzaroli, 1948) can be compared with the above specimens. However, the specimens from Bacton and West Runton are larger than this subspecies; moreover those from West Runton are certainly younger, and this is probably true also for those from Bacton and Trimingham.   After the close of the Villafranchian, no deer of this size is known until the Clacton stage.
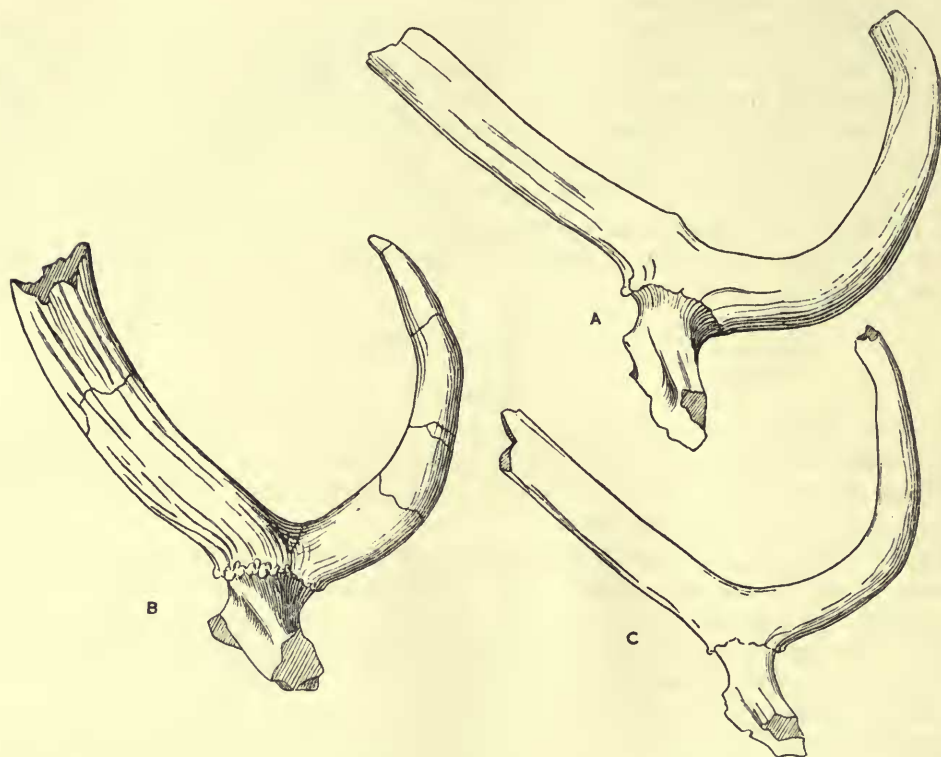
FIG. 50.   Cervid cf. *Dama clactoniana*, right antlers. ¼ natural size. A. Abnormal specimen, Bacton, very old ? B.M. (G.D.), Savin 1283. B. Abnormal specimen, very old ? West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 554. C. Trimingham, B.M. (G.D.), M. 6367.

In this horizon we find in East Anglia *Dama clactoniana* (Bate, 1938, Oakley & Leakey, 1938), with which the fragments described above may be identified.

Keilhack (1888) described a pair of antlers of a large fallow deer from Belzig, near Berlin, which he supposed to belong to the Lower Pleistocene or even to the preglacial. But the occurrence of *Alces* in the same deposit points to an Upper Pleistocene age.

Species incorrectly recorded from the Forest Bed

" *Cervus* " *polignacus* Robert

1882. *Cervus polignacus* Robert : Newton, p. 59.
1891. *Cervus polignacus* Robert : Gunn, pl. 1, fig. 94, pl. 2, fig. 95.
1891. *Cervus polignacus* Robert : Newton, p. 29, pl. 4, fig. 12.

Newton, on Falconer's authority, referred to *Cervus polignacus* two imperfect antlers characterized by a low brow tine, branching at a very wide angle from the beam. These two specimens have been figured by Gunn and are now in the Norwich Museum. Several more imperfect antlers in the same museum have been referred to this species, and in the British Museum I have seen other fragments of a similar type. One of them, of a rather small size, has been incorrectly identified with *Megaceros savini* by Dawkins (1887, pl. 3, fig. 2). All these fragments are very unsatisfactory and are susceptible of different interpretations.

The name *Cervus Dama polignacus* was given by Robert (1829) to two incomplete skeletons from Solilhac: one of them is identical with his *Cervus solilhacus* (now *Megaceros solilhacus*) from the same locality. The second is a small red deer with abnormal characters; Pomel (1853) named it *Cervus roberti*.

" *Cervus* " *carnutorum* Laugel

A fragment said to come from the Chillesford Clay at Aldeby, identified with *Cervus carnutorum* and figured by Dawkins (1872), may either belong to a large specimen of *Euctenoceros falconeri*, or to *E. sedgwicki*. Three specimens from the Norwich Crag quoted by Newton (1891, p. 26, pl. 4, fig. 3) possibly belong to *E. falconeri*. Other specimens from the Forest Bed determined as *Cervus carnutorum* in the collections belong to *E. sedgwicki*.

The name *carnutorum*, like *polignacus*, should be dropped (Stehlin, 1912).

Alces alces L.

1891. *Alces ?*   Gunn, pl. 6, fig. 4.

A much rolled antler of *Alces alces*, from an unknown locality, has been figured by Gunn. Its fossilization is less advanced than that of the other specimens, and no doubt it came from a younger horizon.

Megaceros giganteus Blumenbach

1882. *? Cervus megaceros* Hart : Newton, p. 58.

Although this species was recorded from the Forest Bed by the earlier authors, Newton excluded it.

An isolated P_4 from Sidestrand, in the Savin collection, registered B.M. (G.D.), Savin 1601, might possibly belong to this species, but its occurrence in the Forest Bed can be excluded.

Rangifer tarandus L.

1891. *Cervus* sp. Gunn, pl. 6, fig. 3.

A much-rolled fragment of an antler, found on the beach at Pakefield, belongs to this species. Gunn questioned whether it belonged to the Forest Bed Fauna, and it can be excluded.

CHRONOLOGY

The Characters of the so-called Forest Bed Fauna

The so-called Forest Bed Fauna is very abundant in species, and includes representatives of faunas met with at different horizons in continental Europe. This unusual assemblage has been explained in various ways. Whereas the older authors favoured an Upper Pliocene age (Reid, 1890, with bibliography), or assumed that this fauna was partially or totally derived (Dubois, 1905), more recent authors (Osborn, 1922, followed by Zeuner, 1945) attributed the whole fauna to the early Pleistocene (post-Villafranchian), and interpreted the archaic species as relics. Zeuner distinguished a " Cromer Forest Bed," where these archaic representatives are found, and a " Bacton Forest Bed " without archaic elements, which he thought to be a little younger.

All these interpretations are untenable. A Pliocene age is ruled out by the presence of species which immigrated into Europe after the close of Villafranchian times. On the other hand, the older representatives, once attributed to the Pliocene but actually of Upper Villafranchian age, do not constitute isolated relics; an entire faunal assemblage characteristic of that period is present. Moreover, primitive species occur together with their more advanced descendants, and Zeuner's " Cromer Forest Bed " is richer in species than any other locality. The deer, according to the present revision, include 15 species, and we cannot imagine that they lived at the same time. A derived fauna can also be excluded, as the fossils consist for a large part of large antlers of deer, jaws and limb-bones of elephants, all of them heavy and brittle, but rather well preserved. This is true both for the older and for the younger representatives of the fauna.

The alternative solution, namely, that the deposit includes several horizons, has been discussed in a previous section (" Geology "), and affords the only satisfactory explanation of the mixed character of the " Forest Bed Fauna." An attempt will be made here to determine the stratigraphical range of the 15 species of deer. It will be useful, however, first to illustrate the time scale we shall use for comparison.

Faunal changes during the Lower and Middle Pleistocene

The Pleistocene continental sequence is marked by widespread faunal changes, consisting of extinctions of old forms, immigrations of new forms and evolution of primitive species into more advanced ones *in situ*.

Following the resolution made by the International Geological Congress in London (1948), we shall place the Calabrian, and its continental equivalent, the Villafranchian, at the base of the Pleistocene. However, it is now generally realized that

the so-called main Villafranchian fauna does not constitute such a uniform assemblage as former authors assumed, and that it ranges over a relatively long lapse of time.

The well known faunas of the pumiceous sands and conglomerates of the Montagne de Perrier in Auvergne (Ravin des Etouaires, Roca Neyra, Pardines) are older than any of the other faunas hitherto attributed to the Villafranchian, and their inclusion in this stage is misleading. These faunas are broadly contemporaneous with those of the Roussillon (Depéret, 1897) and of the first lacustrine phase of the Upper Valdarno (lignites with *Tapirus arvernensis* and laminated clays with plants; see Merla, 1949 : 51–57). In the Montagne de Perrier two horizons can be distinguished (Jung, 1946), but according to Prof. Bout of Le Puy (private information) there is no break in the sequence and the series seems to range over a short interval of time. In the three localities recorded above there is no trace of the cold climatic phase that marks the beginning of the Pleistocene.

The fauna of the immediately following cold phase is perhaps represented in the solifluction deposits of Vialette, in the highlands of southern France (see Bout & Cailleux, 1951). In my opinion this cold phase might correspond to the Günz glaciation and marks the beginning of the Pleistocene.

In the Upper Valdarno basin the first lacustrine phase is overlain uncomformably by a second lacustrine series (Merla, 1949), and to this only is the term Villafranchian generally applied by Italian geologists. Its lower portion, not exposed, has been explored by borings and has yielded a flora that seems to indicate a cold climate. In the exposed section probably two horizons can be distinguished palaeontologically, a lower horizon with *Mastodon arvernensis* and an upper horizon with *Elephas meridionalis*, although these two species may have lived together for a short period (Merla, 1949; Azzaroli, 1950).

The fauna of Olivola (Azzaroli, 1950) is contemporary with the lower section with *Mastodon*, that of Tegelen (Hooijer, 1947) with the upper section with *Elephas*. The latter, according to Woldstedt (1950, " Tegelenschichten ") is of an immediately pre-Elster age, that is, it belongs to the Günz-Mindel interglacial.

The end of this period is probably represented by the faunas of some solifluction deposits of southern France (Bout & Cailleux, 1951; Bout & Azzaroli, 1953, and private information from Prof. Bout). Sénèze (Schaub, 1944) is perhaps the most celebrated of these deposits.   Other localities are Sainzelles and the Creux de Peyrolles. Perhaps also the loessic deposit of St. Vallier (Viret, 1948) should be placed here. These faunas are decidedly younger than that of Vialette and may be correlated with the Mindel glaciation, that marks therefore the close of the Villafranchian.

In England the Pleistocene starts with the Red Crag (Lagaaij, 1952).   The mammalian fauna of this horizon is represented by poor fragments, among the most interesting of which are *Mastodon arvernensis*, *Elephas* cf. *planifrons*, two species of *Megaceros*, and *Euctenoceros falconeri*. This horizon presumably corresponds to the unexposed section of the Villafranchian Valdarno series. The equivalent of the highest section of the same series, and of the clays of Tegelen, is represented in England by the Weybourn Crag of Norfolk (see also later).

It is no easy task to state the fate of all the species of the main Villafranchian fauna, as the relationships of many of them with the representatives of later faunas are not yet clear. *Sus strozzii, Euctenoceros ctenoides, E. dicranios, E. tetraceros, Dama nestii,* " *Cervus* " *philisi* and its allies, *Meganthereon meganthereon, Brachyprosopus vireti, Gazellospira torticornis, Nemorhoedus meneghinii, Procamptoceras brivatense, Nyctereutes megamastoides* and *Acinonyx pardinensis* have left no descendants in the later faunas. This is possibly true also for *Leptobos;* a doubtful *Leptobos,* however, has been recorded from Süssenborn (Merla, 1949 : 49). The destiny of the horses is less clear, as this group still needs revision (Stehlin, 1932–33 : 51 ff.). The same difficulty arises for many carnivores; *Epimachairodus* survived for some time, and the larger felids, canids and bears might perhaps have evolved into more modern species (Stehlin, 1932–33, Schaub, 1949). The voles, represented in the Villafranchian by the primitive *Microtus,* underwent a gradual evolution which sets them among the most useful leading fossils for the Lower and Middle Pleistocene (Hinton, 1926; Schreuder, 1936, 1943, 1950; Heller, 1933, 1939; Van der Vlerk & Florschütz, 1950). A similar evolution was carried out by the elephants, although things are here less simple than they were thought at first (Trevisan, 1953). Also *Libralces* seems to have evolved further (see section " Palaeontology "). *Dicerorhinus etruscus* has been recorded also from post-Villafranchian deposits, but is represented there by more advanced forms (Soergel, 1923). *Hippopotamus* is found in the Villafranchian and in later times; its history may be one of successive immigrations and retreats (Stehlin, 1932–33). *Macacus* and *Castor* also survived, but their remains do not indicate whether they underwent any great change. *Trogontherium boisvilletti* seems to have survived unchanged in France and the British Isles (Schreuder, 1951).

The following phase is marked by the immigration of new faunal elements from Eastern Europe or from Asia: primitive red deer (*Cervus acoronatus, C. benindei* and other poorly known forms), the roe, wild boars of the group of *Sus scrofa* (probably represented by a distinct variety; Soergel, 1923), *Gulo gulo, Bos primigenius, Bison priscus.*

The voles evolved from *Mimomys* into primitive *Arvicola* (*A. greeni, bactonensis, mosbachensis*). A primitive *Microtus* has also been recorded from Mosbach. *Libralces* seems to have evolved from *L. gallicus* into *L. reynoldsi,* and the elephants from *Elephas meridionalis* into various races of *E. antiquus* and *E. trogontherii.* The group of *Megaceros verticornis* flourished in this period and possibly evolved *in situ.* Probably also the rhinoceroses and many carnivores are descendants of Villafranchian ancestors.

The best representatives of this period are the main faunas of Mosbach and Süssenborn, and the fauna of Mauer, in Germany; the fauna of Tiraspol in Bessarabia (Pavlow, 1906); the Needian of the Netherlands (Van der Vlerk & Florschütz, 1950), and some fossiliferous sands in the Upper Valdarno, around the village of Bucine (horizon 3 in Merla, 1949 : 51). These sands overlie comformably the Villafranchian, with the interposition of a series of barren gravels. In England the equivalent of these deposits is represented by the estuarine section of the Forest Bed series.

The dating adopted here is in contradiction with some current views and needs explanation.

Soergel (1928) assumed an early Mindel, if not even a pre-Mindel age for the fauna of Mauer.   This was deduced from the occurrence of five horizons of weathered loess above the fossiliferous sands—a rather unsafe way of arguing, inasmuch as the age of the deposit depends on the number of glacial phases we admit.   Soergel assumed two stages in the Würm (Weichsel) glaciation, two in the Riss (Saale) and two in the Mindel (Elster); but recently Woldstedt (1950) described four phases in the Weichsel glaciation and three in the Saale.   These are sufficient to explain the occurrence of even more than five horizons of weathered loess above deposits of the great interglacial, and any evidence for attributing Mauer to the Mindel glaciation falls short.   On the other hand, positive evidence for attributing these faunas to the Mindel-Riss interglacial is afforded by the Needian of the Netherlands, which corresponds to the *Paludina*-beds representing the great interglacial in Northern Germany (Woldstedt, 1950).

In 1932 Solomon placed the Forest Bed series of Norfolk in the first interglacial and assumed that the overlying glacial drift included representatives of the Mindel (North Sea Drift), Riss (Great Eastern) and Würm (Little Eastern) glaciations. But some of the difficulties met with in identifying Solomon's North Sea Drift with the Mindel glaciation and with the Norwich Brickearth of southern Norfolk were stressed a year before by Boswell (1931), and were given again by Boswell and by Hazzledine Warren in the discussion following the presentation of Solomon's paper.   Solomon's evidence of a Mindel-Riss horizon within the glacial drift, assumed to be afforded by his " mid-glacial sands," is not conclusive, as these sands are barren and form no continuous horizon.   In the dating adopted here the second (Mindel) glaciation falls between the Weybourn Crag and the Estuarine Bed.   Its deposits, represented in southern Norfolk by Boswell's Norwich Brickearth, may have been cut out in north Norfolk by the erosion at the base of the Estuarine Bed.

The distribution of the *Bovidae* seems to have been influenced by geographic or climatic factors.   The bison is recorded at Mauer, Mosbach and Süssenborn, whereas the aurochs makes its appearance in Central Europe during the Riss glaciation (probably in a mild interstadial).   On the other hand this species is not uncommon in the sands near Bucine in the Upper Valdarno, with *Cervus* cf. *elaphus* and *Elephas antiquus*, which, from their position, cannot be much younger than the Villafranchian, whereas the bison is recorded in Italy only from the Upper Pleistocene.   Possibly *Bos* immigrated into Italy along the southern slope of the Alps, whereas for some unknown reason it avoided Central Europe, and *Bison* did the reverse.   In the gravels of Tiraspol, with a faunal assemblage characteristic of the stage of Mauer and the upper sands of the Upper Valdarno, *Bos* and *Bison* occur together.   Unfortunately *Bos* is represented only by limb bones (Pavlow, 1906).

A later phase is marked by the appearance of more advanced species of *Arvicola*, evolved *in situ*, and by a widespread occurrence of *Microtus*, probably immigrants; but there does not seem to be any well-marked break in the fauna.   *Dama clactoniana*, recorded only from the British Isles, belongs to this period.

The incoming Riss (Saale) glaciation seems to have extinguished *Dama clac-*

toniana and many species of the group of *Megaceros verticornis*. *Elephas primigenius*, or a related form, occurs for the first time at the beginning of this phase, but became common only after a mild oscillation, well marked at Steinheim a.d. Murr. In this mild interstadial the giant deer are represented here by *Megaceros antecedens* (Berckhemer, 1941) and the red deer by *Cervus elaphus angulatus* (Beninde, 1937). In the following cold phase the red deer is represented by a modern form and *Coelodonta antiquitatis* makes its very first appearance as an immigrant. The date of the immigration of the reindeer is less clear. Soergel (1943) recorded it from Steinheim, Mosbach and Süssenborn, but I have been unable to check the dating of these specimens. They are all said to belong to the tundra group (*R. arcticus*). Also *Ovibos moschatus* has been recorded from Süssenborn (Soergel, 1941).

At the end of the Riss glaciation (late Drenthian) the voles are represented by modern forms. A good guide fossil for the post-Rissian is *Megaceros giganteus*.

The Distribution of the Deer of the Norfolk Coast and their value for Stratigraphy

As stated above, the deer of the Forest Bed series *sensu lato* include representatives of different faunas. Two faunas are quite distinct, whereas the existence of a third fauna is vaguely indicated by the deer, and is demonstrated conclusively only by other mammals.

The earliest fauna belongs to the upper section of the Villafranchian. It can be correlated with the horizon of Tegelen, Sénèze, and the ferruginous sands of the Upper Valdarno, and is represented by *Libralces gallicus*, *Euctenoceros tetraceros*, *E. ctenoides*, cervid cf. *Dama nestii nestii*. This fauna occurs in the Weybourn Crag.

The second fauna belongs to the second interglacial and corresponds stratigraphically to the classic faunas of Mosbach (main fauna), Mauer, Süssenborn (main fauna) and Tiraspol. Its representatives are *Libralces reynoldsi*, *Cervus* cf. *elaphus*, *Megaceros verticornis*, *Capreolus capreolus*. This fauna occurs in the Estuarine Section of the Forest Bed.

The third fauna, corresponding to a later horizon of the same interglacial, is probably indicated by *Dama clactoniana*, associated with *Cervus* cf. *elaphus*, *Megaceros verticornis*, *Capreolus capreolus*. This fauna occurs, partly at least, in the Upper Freshwater Bed. Possibly there is no true break between the two younger faunas.

The distribution of these species is not uniform throughout the outcrop of the Forest Bed series *s.l.* The Villafranchian species are restricted to the western section of the outcrop; they are very common at East Runton, where they are not accompanied by later faunal elements, and at Sidestrand, associated with younger species; rare at West Runton, Overstrand and Mundesley. Some doubtful and much-rolled specimens have been found also at Pakefield, at the eastern extreme of the outcrop. The second fauna occurs in all the localities, with the exception of East Runton, where only a few much-rolled specimens have been found.

The poorly represented fallow deer, supposed to represent the third fauna, is recorded from Bacton, Trimingham, and from the Upper Freshwater Bed at West Runton. Other representatives of this fauna have been recorded by Hinton from the Upper Freshwater Bed at Bacton and West Runton (see later), but this fauna might be more widespread.

Many localities have therefore yielded a mixed fauna, whereas a few of them have yielded more uniform faunas. Of particular interest are East Runton, with a pure Villafranchian fauna, and the Upper Freshwater Bed of West Runton, which, also on geological grounds, can be assumed to include only representatives of the "third" fauna. This distribution may give a clue to an approximate dating of the remaining species, not known or doubtful in other districts.

Libralces minor is recorded only at East Runton and Sidestrand; it belongs therefore to the Villafranchian fauna.

Libralces latifrons from Happisburgh (doubtful at Mundesley, Cromer and Walcot) may belong either to the second or the third fauna.

Euctenoceros sedgwicki, from Bacton and Mundesley, probably belongs to the second fauna. The presence of the large fallow deer and the absence of *Libralces reynoldsi* at Bacton would rather suggest a later age, but the absence of *E. sedgwicki* in the very fossiliferous Upper Freshwater Bed of West Runton is, perhaps, more significant. This species is possibly present also at St. Prest.

Megaceros dawkinsi and *M. savini* are probably of the same age. They do not occur in the Upper Freshwater Bed of West Runton, nor at East Runton. *M. dawkinsi* has been recorded also from the Weybourn Beds at Weybourn by Savin, but the name of the horizon was possibly taken from the locality and it would be unsafe to rely on this statement. This species, or a related form, seems to have been widespread in continental Europe.

The dating of "*Cervus*" *obscurus* is more doubtful, but this species probably belongs to the second interglacial.

The Evidence Afforded by Other Mammals on the Age of the Forest Bed Series

The list of the other mammals from the Forest Bed *s.l.* also gives the impression of a mixed fauna. We need only mention the occurrence of four species of elephants, a fact not recorded from any other locality in Europe.

The elephants still need revision, and it would be unsafe to assume the alleged *Elephas primigenius* as evidence of the existence of an early Rissian horizon in the Forest Bed series. But the evidence afforded by the voles (Hinton, 1926; 1926a) is more conclusive, and demonstrates the existence of an horizon equivalent to the Swanscombe gravels.

The "shelly crag" at East Runton yielded Villafranchian representatives (*Mimomys pliocaenicus*, *M. intermedius*, *M. savini*), whereas the Upper Freshwater Bed at West Runton yielded a mixed fauna: *Mimomys intermedius*, *M. savini*, *M. maiori*, *Evotomys* sp., *Pitimys arvaloides*, *P. gregaloides*, *Microtus arvalinus*, *M. nivalinus*, *M. nivaloides*, *M. ratticeppoides*. This is certainly not evidence of

the presence of different horizons in the Upper Freshwater Bed, as the older species may easily have been washed in. The age of the deposit is indicated by the younger species and corresponds to the early Drenthian (Van der Vlerk & Florschütz, 1950). The same species of *Microtus* have been found also in the middle gravels of Swanscombe (Schreuder, 1950). A correlation between the Upper Freshwater Bed and Swanscombe has been made also by Hinton (1926a, 336–337). Shortly later Mochi (1929 : 179–181) proposed a correlation of the Norfolk sequence with the earliest glaciations that agrees substantially with that stressed in these pages and differs only in minor details.

SUMMARY

GEOLOGY AND CHRONOLOGY. The mammal bearing horizons of the Norfolk coast include three horizons separated by unconformities : the Weybourn Crag, the Estuarine Bed or Forest Bed *s. str.* and the Upper Freshwater Bed. The whole series rests on a levelled surface of chalk and is capped by glacial drift. The so-called Forest Bed Fauna is actually made of three successive faunas. The oldest one, from the Weybourn Crag, is of upper Villafranchian age and is assumed to correspond to the first (Günz-Mindel) interglacial. Its representatives are : *Euctenoceros ctenoides*, *E. tetraceros*, *Libralces gallicus*, *L. minor*, and a small species perhaps identical with *Dama nestii nestii*. The second fauna, from the Estuarine Bed, is contemporary with the main faunas of Mosbach, Süssenborn, Mauer, Tiraspol, and the horizon of Neede, and is assumed to correspond to the second interglacial. Its representatives are : *Megaceros verticornis*, *M. dawkinsi*, *M. savini*, *Libralces reynoldsi*, *Cervus* cf. *elaphus*, *Capreolus capreolus*, and possibly *Libralces latifrons*, *Euctenoceros sedgwicki* and "*Cervus*" *obscurus*. The third fauna, from the Upper Freshwater Bed and possibly also from the highest section of the Estuarine Bed, is contemporary with the gravels at Swanscombe and with the early Drenthian and corresponds to a later period of the same interglacial. It is represented by a species possibly identical with *Dama clactoniana*, together with *Megaceros verticornis*, *Cervus* cf. *elaphus* and *Capreolus capreolus*. Conclusive evidence of its age is afforded by small rodents.

PALAEONTOLOGY. *Alcinae* and *Capreolinae* were differentiated from the *Cervinae* before the Upper Miocene. The Upper Miocene *Cervinae* belong to two quite distinct lineages. In eastern Europe they are represented by *Damacerus bessarabiae* (= *Cervocerus novorossiae*) and *D. variabilis* (= *Procervus variabilis*), and may perhaps have evolved into the Villafranchian *Cervus ramosus*. In China they are represented by three-tined deer (incorrectly identified with *Cervocerus novorossiae* by former authors), from which probably most of the Pleistocene and living *Cervinae* took origin. The phyletic development of antlers is also discussed.

The deer of the Weybourn Crag and Forest Bed *s.l.* belong to the genera *Libralces*, *Capreolus*, *Cervus*, *Euctenoceros*, *Megaceros* and possibly *Dama*; there is in addition a species of *Cervinae* of uncertain affinities.

Libralces is a close ally of *Cervalces*. *L. gallicus* is smaller than living elks, but *L. reynoldsi*, which is probably its descendant, is the largest deer hitherto known. *L. latifrons* and *L. minor* are poorly represented.

The roe also is poorly represented.

The earliest representatives of *Cervus s. str.* were more primitive than the living European red deer; some of them were similar to living red deer of Central Asia. The red deer of the Forest Bed also seem to be primitive, but their remains are not satisfactory.

Euctenoceros is distinguished by peculiar features of the antlers. Its most primitive representative is *E. falconeri* from the Red Crag. *E. sedgwicki* is possibly its descendant. *E. ctenoides* (= *E. teguliensis*) and *E. tetraceros* do not differ from the types from other Villafranchian localities.

Megaceros can be divided into two groups, based on characters of the skull and antlers: the group of *M. giganteus* and the group of *M. verticornis*. *M. savini* is a primitive species of the group of *M. giganteus* and its antlers are not palmated. *M. verticornis*, the commonest species of deer in the Forest Bed, has large and widely palmated antlers. *M. dawkinsi* belongs to the same group; it is smaller and has secondarily reduced antlers, and a hypsodont dentition.

" *Cervus* " *obscurus* is a large species of quite unusual features and of unknown affinities. Its remains are scanty.

Two much smaller species may possibly be identified with *Dama nestii nestii* and with *Dama clactoniana*.

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